Psychological and Neural Processing of Social Risk and Discrepancy in Major Depressive Disorder

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DECLARATION

This thesis is the result of my own work and includes nothing which is the outcome of collaboration except as specified in the text. It is not substantially the same as any work that has already been submitted before for any degree or other qualification except as specified in the text. It does not exceed the prescribed word limit for the Clinical Medicine Degree Committee.

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ABSTRACT

Major Depressive Disorder (MDD) is one of the most prevalent health conditions in the world, characterised by persistent low mood and disruption to education, relationships, and employment. Disruption to social functioning is a core feature of MDD, and this dimension of the disorder may offer valuable insight into its aetiology. This thesis aims to extend our understanding of social processing in MDD by testing hypotheses generated from a socio-evolutionary theoretical framework of MDD, with particular emphasis on the Social Risk Hypothesis of Depressed Mood, which conceptualises depressed mood as an adaptive response to elevated risk of social exclusion. The thesis pursues these aims utilising novel protocols and neuroeconomic games to examine social risk-taking and self-discrepancies, and by examining the role of regions of the physical pain network in social function and processing of unexpected social information. The thesis consists of nine chapters; one general methodology chapter (Chapter 3), five chapters detailing novel experimental studies (Chapters 4,5,6,7 and 8), one describing a reanalysis of existing data (Chapter 2), one introductory chapter and one discussion chapter (Chapters 1 and 9 respectively). Across these chapters, the thesis presents neural and behavioural evidence that MDD is associated with reduced social risk-taking, increased sensitivity to an exclusion-relevant context (in-group interactions) and stronger enforcement of social norms. The thesis presents neural evidence of a negative processing bias for self-discrepancies in MDD, linked to activation in the dorsal anterior cingulate cortex and anterior insula, and suggesting a role for perfectionism as a transdiagnostic sensitivity to such discrepancies. Suggestions for future research are discussed, including increased utilisation of neuroeconomic games, particularly in relation to assessing social function as a transdiagnostic marker. Overall, the thesis provides support for socio-evolutionary frameworks of affect, and highlights their unique perspective for understanding affective disorders, with some ‘deficits’ usefully reconceptualised as adaptive mechanisms.

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ABBREVIATIONS

AI	Anterior Insula
dACC	dorsal Anterior Cingulate Cortex
ANOVA	Analysis of Variance
AnG	Angular Gyrus
BAI	Becks Anxiety Inventory
BART	Balloon Analogue Risk Task
BDI	Becks Depression Inventory
fMRI	functional Magnetic Resonance Imaging
IPSM	Interpersonal Rejection Sensitivity
MDD	Major Depressive Disorder
PGG	Public Goods Game
ROI	Region of Interest
SIP	Social Investment Potential
SRH	Social Risk Hypothesis
UG	Ultimatum Game

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CHAPTER 1. A SOCIO-EVOLUTIONARY FRAMEWORK OF DEPRESSION: THEORETICAL BACKGROUND AND LITERATURE REVIEW

1.1. AIMS

The work described in this thesis aims to extend our understanding of social processing in depressive disorders by addressing gaps in the existing psychological and neural literatures. At the neural level, it aims to expand our understanding of the role of regions of the physical pain network in social function, by investigating their relationship with unexpected socially salient information. At the behavioural level, it aims to address the previously under-researched domains of social risk-taking and self-discrepancy, through the utilisation of novel protocols and neuroeconomic games. These investigations aim to test hypotheses generated from, and to be interpreted within, a socio-evolutionary theoretical framework of depression, and contribute to a wider discussion regarding the contribution of social function to affect and psychological disorders.

Outline

This thesis consists of nine chapters reporting work investigating neural and behavioural domains of social processing in depression. The present chapter – Chapter 1 – provides an overview of socio-evolutionary theories of affective disorder, with particular relation to depression, and explores our current understanding of their neural basis. We discuss the potential contribution of neuroeconomic paradigms to social decision-making, establishing a basis for their implementation in subsequent chapters.

Chapter 2 details a reanalysis of imaging data acquired by Dalgleish et al. (2017) during a social feedback task, with the purpose of isolating the neural signature of discrepancies between one's self-evaluation and the evaluation of others. This preliminary investigation informs the subsequent protocol and focus of the thesis.

Chapter 3 provides a general overview of the protocol utilised in this work, which applies a range of behavioural and imaging tasks in a depressed and matched control sample. This chapter also characterises the sample with reference to measures of perceived social status and behaviour, such as subordination and submissiveness.

Evolutionary theories of depression generate hypotheses regarding both how social rank is determined, and how adaptive defensive (depressogenic) behaviours can be activated in response to critically low rank; this thesis considers these elements in turn. First, Chapters 4 and 5 detail two neuroimaging paradigms designed to investigate the functional and neural signatures of establishing one's social rank, as a function of self-discrepancies. Chapter 4 will investigate discrepancies between concepts of self, while Chapter 5 considers discrepancies between one's self-rating and the ratings of others.

Next, Chapters 6, 7 and 8 detail neuroeconomic paradigms designed to assess social risk taking and cooperative behaviours. Chapter 6 utilises the Ultimatum Game (UG), a well-established task for investigating fairness and cooperation, and explores the neural response to these salient social experiences, alongside behavioural data. Chapter 7 reports a Public Goods Game (PGG), a measure of cooperation within groups, and additionally considers the role of punishment in social behaviour. Chapter 8 applies a novel social adaptation of an established behavioural measure of risk-taking, the Balloon Analogue Risk Task (BART), and discusses the relevance of these findings within an evolutionary framework.

Finally, Chapter 9 provides a general discussion of the work presented in this thesis within a socio-evolutionary context and considers its implications for our understanding of social function as a transdiagnostic marker and its role in the etiology of depression, in addition to summarising suggestions for future theoretical and behavioural work.

1.2. DEPRESSION

For the purpose of the research in this thesis we have recruited a depressed sample who meet criteria for a diagnosis of Major Depressive Disorder (MDD) according to a structured clinical interview. MDD is a psychiatric disorder characterised by persistent low mood and feelings of sadness, low energy (anergia), and a loss of pleasure or interest in daily activities (anhedonia) (DSM-V; American Psychiatric Association (APA), 2013). These symptoms are associated with profound impairments in social, occupational, and functional domains, and incidence of MDD is linked with disruption to education, marital status, and employment (Kessler, 2011). The detriment to perceived health associated with MDD is greater than that associated with cancer, cardiovascular disorders (Alonso et al., 2011), arthritis or diabetes (Moussavi et al., 2011). MDD is one of the most prevalent health conditions in the world, affecting more than 300 million people, and is the third leading cause of years lived with disease worldwide (Global Burden of Disease Study, 2017). Moreover, MDD is the leading cause of death by suicide (Ferrari, 2013), with half of all completed suicides linked to depressive or mood disorders (ICD-10 F3). In 2019, the World Health Organisation documented over 700,000 suicides worldwide, accounting for 1.3% of premature deaths, with 77% occurring in low- and middle-income countries (WHO, 2020). While prevalence of MDD is nearly twice as high in women than in men (Albert, 2015), with gender differences peaking in adolescence (Salk, Hyde & Abramson, 2017), rates of suicide are 2.3 times higher in males (WHO, 2020).

Diagnostic criteria for Major Depressive Disorder according to the Diagnostic and Statistical Manual 5th Edition (DSM-5, American Psychiatric Association (APA), 2013) are presented in Appendix 1.1. Individuals must present with at least one of either depressed mood, defined as a feeling of sadness or hopelessness lasting most of nearly every day, or anhedonia, a loss of interest or pleasure in activities. Individuals must experience at least five symptoms, which

might include changes in weight or appetite, sleep disturbance, fatigue, psychomotor disturbances, difficulty with concentration or decisiveness, feelings of guilt or worthlessness, and suicidality. These symptoms must cause significant distress or impairment of functioning to be diagnostically relevant. The DSM-5 allows 14 subcategories of MDD diagnosis, for example with psychotic or catatonic features, as well as endogenous and reactive subtypes. Additionally, this edition was the first to introduce new specifiers, such as mixed features, which allows for manic symptoms, and anxious distress, which overlaps significantly with symptoms of GAD and panic. These are combined with a range of seven severity descriptors (Uher, Payne, Pavlova & Perlis, 2014). This complexity serves to illustrate the heterogeneity of symptoms in MDD, and the varied functional domains affected.

Social Functioning

Disruption to social functioning is a core feature of MDD (Kupferberg, Bicks & Hasler, 2016). Individuals with MDD show increased sensitivity to signals of social rejection, experiencing greater and more prolonged changes in affect (Platt et al., 2013). At a neural level, social rejection elicits greater activity in the insula, an area associated with emotional pain and salience (Silk et al., 2014), and lower activity in the dorsolateral Prefrontal Cortex (dlPFC), associated with emotional regulation (Hooley et al., 2005) in MDD. Accordingly, MDD patients are significantly more distressed by interpersonal problems than never-depressed samples (Barrett & Barber, 2007). Alongside altered rejection sensitivity, MDD is associated with blunted sensitivity to social reward (Pizzagalli, 2014; Alloy al., 2016), which is reflected in reduced neural responsiveness (Olino, Silk, Osterritter & Forbes, 2015; Oumeziane, Jones & Foti, 2019). This may explain why individuals with MDD show reduced motivation to engage in social interactions (Hsu et al., 2015) and obtain social rewards (Brinkmann et al., 2014), sometimes termed social anhedonia (Kupferberg et al., 2016).

MDD is also associated with deficits in socio-cognitive processes in the domains of executive function, attention, and memory (Christopher & MacDonald, 2005; Zhang et al., 2018; Roiser & Sahakian, 2013). Deficits in lower-order social cognition include difficulty recognising facial emotions (Csukly, Czobar, Szily, Takacs & Simon, 2009) and a mood-congruent facial processing bias (Anderson et al., 2011). This extends to higher-order social processing deficits, including difficulties in affective Theory of Mind tasks (Weightman, Air & Baune, 2014), social perception (Elliot et al., 2011) and metacognition (Ladegaard et al., 2015). Accordingly, individuals with MDD more frequently report difficulties in social relationships (Hirschfeld et al., 2000), while cognitive therapies for MDD produce concomitant improvements in social-interpersonal functioning (Vittengl, Clark & Jarrett, 2004) and reductions in interpersonal distress (Quilty et al., 2013).

Importantly, many of these features are not unique to MDD. Social anhedonia is observed in Bipolar Spectrum Disorders (BSD) (Akiskal et al., 2006) and schizophrenia (Dodell-Feder et al, 2014), reduced social reward sensitivity is observed in BSD (Alloy et al., 2015; Dutra, Cunningham, Kober & Gruber, 2015), while heightened sensitivity to social rejection is observed in borderline personality disorder (Gutz et al., 2015), and anxiety (Kir et al., 2021). In view of these and similar findings, and of the high degree of comorbidity amongst depressive and affective disorders (Jacobsen & Newman, 2017), altered social functioning might be a useful factor in the development of transdiagnostic treatment frameworks (Barkus & Badcock, 2019). Accordingly, the pan-European PRISM study identified social dysfunction and its most evident clinical expression of social withdrawal as the key target dimension for future transdiagnostic research (Kas et al., 2019; Porcelli et al., 2019). Moreover, this points to a possible shared underlying role in the etiology of these disorders, which is explored in the evolutionary theories discussed in this chapter.

1.3. EVOLUTIONARY THEORY

Evolutionary theories of mental health have grown in prominence in recent years (Durisko et al., 2016; Tavares, Lima & Tokumaru, 2021) yet were initially proposed nearly 30 years ago (McGuire, Marks, Nesse & Troisi, 1992). In the simplest terms, an evolutionary theory assumes that behaviours seen in clinical mental health disorders are driven by mechanisms which must have been adaptive to survival during the Environment of Evolutionary Adaptedness (EEA) (Tooby & Cosmides, 1992). In the modern world, such mechanisms may be acting outside of their ideal adaptive range, however, considering the functional basis of such behaviours provides greater insight into their etiology, and an alternative way of viewing mental ill health that may generate novel treatment options.

Affective states are an appropriate target for such evolutionary models; their mechanism shows specificity in terms of inputs, being activated by specific contexts, and outputs, either behavioural, cognitive, or physiological (Oatley, 1992). Moreover, these states are ubiquitous in humans, being represented across cultures and geographies (Jenkins, Kleinman & Good, 2013). Considering affective disorders from an evolutionary perspective allows an integrative approach to their analysis, incorporating social, biological, and functional considerations (Hagen, 2011). Additionally, understanding the evolutionary advantages that contribute to the etiology of such disorders may be practically valuable for clinicians in distinguishing between functional and dysfunctional forms of depression.

Many of these theories have focused on the importance of social relationships; during the Pleistocene period (2.6m-12,000 years ago), in the human EEA, membership of a social group conferred access to several resources crucial to reproductive fitness. These include dyadic mating relationships, as well as group-based advantages such as protection from predators or group foraging and hunting strategies (Nowak & Highfield, 2011). Access to these resources

is dependent on the individual's status and alliances within this social context, and exclusion therefore has a clear and significant impact on one's survival and reproductive success.

Social Competition theories of depression developed from this central tenet, that social rank confers access to reproductive resources (Buss, 1999), and conceptualised behaviours associated with depressed mood as a way of deescalating agonistic encounters that might result in a loss of status (Price et al., 1994). Attachment theories (Gilbert, 1992) focus more on the breakdown or failure to establish attachment relationships and posit that depressogenic behaviours serve as a distress call to re-establish bonds (Ingram et al., 1998). Alongside these, Resource Conservation theories consider the inhibition of appetitive functions in depression as a way of adjusting resource allocation in situations of low reward (Nesse, 2000; Seligman, 1975). Individually, these theories struggle to explain the mechanisms by which these functions would operate and be selected for, moreover, several features of depression are left unexplained; Resource Conservation theories are unable to explain the social nature of events precipitating depressed mood (Chen & Feeley, 2014), Social Competition theories often arguably downplay the importance of affiliation in determining social rank (Weisman et al., 2011), while Attachment theory struggles to explain the importance of non-attachment relationships in depression, and seems at odds with the social withdrawal observed in sufferers (Santini et al., 2020).

Social Rank Theory

The Social Rank Theory of Depression (Price and Sloman, 1987; Gilbert, 1992) is an evolutionary theory which proposes that the submissiveness and feelings of inferiority observed in depressed states evolved to de-escalate competitive situations (Gilbert, 2001). Appropriately signalling defeat enables subordinate individuals to limit the aggression of the attacker (Gilbert, 2000), thereby avoiding potential injury or loss of life (Higley et al., 1996).

This subordination response is sometimes termed the Involuntary Defeat Strategy (IDS: Sloman, 2000) and entails feelings of hopelessness, inferiority and weakness that discourage the individual from persisting in conflicts where they perceive a low likelihood of success. Whether a given situation triggers this response or not may be based on the value of the resource and estimations of the relative negotiation or challenging capacity of the competitors,termed Resource Holding Potential (RHP; Gardner & Price, 1999). While perceiving your RHPas low may lead to an adaptive defeat response, chronically low RHP is a contributor to the development of depression (Price et al., 1994). However, agonistic behaviours are only one dimension of the human ability to compete; eliciting help from others through affiliation, attractiveness and prestige are all important factors in building social defences (Barkow, 1989). These factors were subsequently incorporated into the theory as Social Attention Holding Power (SAHP), the ability to elicit positive attention and social rewards from others (Gilbert, 1997). These two strategies occur alongside one another, and failure in either dimension may therefore activate the feelings of shame and inferiority associated with depression (Gilbert, 2000) along with signals of social defeat and subordination.

Sociometer and Hierometer Theories

The influential Sociometer Theory (Leary et al., 1995) was established on the premise of attachment-based theories in this space more generally, that humans have a fundamental need to belong as a result of the adaptive advantages of group membership (Baumeister and Leary, 1995), and therefore evolved psychological systems to support social acceptance. In this theory, self-esteem acts as a “sociometer”, serving two functions; to track an individual’s level of social inclusion, and to motivate affiliative behaviours when social inclusion becomes unacceptably low. By comparison, Hierometer Theory (Mahadevan, Gregg, Sedikies & DeWaal, 2016) proposes that self-esteem tracks not social inclusion but social status, with the purpose of

regulating assertiveness and aiding navigation of social hierarchies. This theory integrates the concept that, while high status may confer fitness advantages (von Rueden et al., 2011), a drive to achieve ever higher status is likely maladaptive given the potential risk of competing with others. Assertive or submissive behavioural strategies can therefore both be adaptive, or maladaptive, depending on the context. A key difference between these two theories is the emphasis on homeostatic vs non-homeostatic mechanisms. While Sociometer Theory posits a minimal threshold for inclusion, with self-esteem functioning to restore one's status when threatened, Hierometer Theory posits that self-regard functions not to adjust one's social status, but rather, to bring one's behaviour in line with the status they currently have. Interestingly, research in this area has indicated that self-regard covaries positively with *both* inclusion and status (Mahadevan, Gregg & Sedikides, 2019).

The Social Risk Hypothesis

The Social Risk Hypothesis of Depressed Mood (Allen & Badcock, 2003) integrates two dimensions of interpersonal relationships; the affiliative dimension, represented in-part by previous Attachment-based theories, and the agency dimension, represented by Social Competition theories, conceptualising both as presenting risks to one's social status.

Social Investment Potential

Given the critical importance of avoiding social exclusion, an ability to estimate one's danger of exclusion has clear adaptive advantages. As excluding someone presents a cost to the group, which loses the resources provided by the individual, one might consider the resources they contribute, or the resources they have potential to contribute in the future (their Social Value) as a key factor in determining their risk of exclusion. However, this value can be negated if the individual is burdensome to the group in other ways (Social Burden). Consequently, the Social

Risk Hypothesis (SRH) posits that the human evolved capacity to reason about risk of exclusion and make social investment decisions integrates both Social Burden and Social Value, into a single value termed Social Investment Potential (SIP).

SIP can be thought of as the ratio between the two factors of Value and Burden. An individual who makes a large contribution to the group, for example through physical resources, skills, energy, or time commitment, will be high in Social Value. If they also represent a low Burden to the group, this individual would be high in SIP. However, if that same individual was a high Burden to the group, and the two values approached equivalence, their SIP would decrease, presenting the possibility of exclusion.

The ability to correctly estimate ones SIP confers several adaptive advantages. An individual who is able to accurately judge the likelihood of success in social endeavours is better able to selectively manage their contributions to those endeavours. For example, when SIP is high, an individual can choose to maximise their return from social investments by demanding more from a relationship or choosing to reinvest resources in other relationships. Crucially, an estimate of one's SIP allows a better understanding of the investments required to achieve one's social goals.

Just as an individual high in financial resources is able to tolerate the possibility of large losses, and can therefore take larger financial risks, an individual's ability to take social risks is predicated on their social resources. An individual high in SIP can afford to engage in social situations with a wide variability of potential outcomes because their risk of exclusion is low, thereby enabling them to seize risky opportunities with greater payoffs. From this individuals' perspective, social situations with uncertain outcomes are opportunities for social gain. However, for an individual low in SIP, a risky situation may result in intolerable costs such as social exclusion. Moreover, if high SIP is based on a high previous rate of success in navigating

social situations, and low SIP on the opposite, the perceived likelihood of success or failure will fluctuate with SIP. Therefore, for an individual low in SIP, it would have been adaptive to adopt a risk-avoidant strategy, in which SIP is raised conservatively through low-risk low-reward interactions. Importantly, the function of this strategy is not to avoid social situations entirely, but rather to avoid situations or behaviours with uncertain outcomes in favour of more certain investments (Allen & Badcock, 2003).

Determining SIP: Social Experiences and Self-Esteem

How, then, does an individual determine whether a loss or change in SIP has occurred? As an evolutionary mechanism, depressed mood is not necessarily triggered by the loss of relationships or threat of exclusion, but rather, by social signals which were associated with such situations during the EEA. We discussed previously how the SRH integrates two dimensions of interpersonal relationships, agency and affiliation. Failure to successfully invest in either dimension may lead to an estimation that SIP is critically low, for example, negative interpersonal feedback, perceptions of entrapment, loss of control, or loss of social status. Figure 1.1 details aspects of the social world which fall into these two domains. As an example of failure in the affiliative domain, insecure attachments with caregivers or romantic partners are related to depressive symptoms (Spruit et al., 2020; Williams & Riskind, 2004), while in the agency domain, lower perceived influence in social interactions is associated with depression (Nezlek, Hampton & Shean, 2000). Previous findings in support of this theory have reported that low social rank is associated with depression (Wood & Irons, 2015) and subjective measures of social status are predictive of depressive symptoms (Euteneuer, 2014; Hoebel et al., 2015). Moreover, social isolation is significantly associated with depression (Matthews et al., 2016; Tawari & Ruhela, 2012), and adverse life events involving social rejection, stress or

loss are major risk factors in the onset of depression (Slavich & Irwin, 2014; Heim & Binder, 2012).

Estimations of one's SIP may also be experienced phenomenologically; according to Sociometer Theory (Leary et al., 1995) self-esteem provides a system for monitoring interpersonal signals of inclusion or rejection. In the context of the SRH, negative social experiences in either the agency or affiliation domains should therefore be associated with lowered self-esteem and predicate depressed mood. Accordingly, the quality and stability of intra-individual relationships has been found to predict trait self-esteem (Denissen et al., 2008), while rejection feedback lowers self-esteem (Bernstein et al., 2013; Zadro et al., 2004). Self-esteem has also been found to vary with an individual's beliefs about whether they possess traits likely to elicit social approval (Anthony et al., 2007) and predictions of how others will react to them (Koch & Shepperd, 2008). Significantly, not only is low self-esteem associated with depression (Schmiz, Kugler & Rollnick, 2003), but longitudinal evidence suggests it is predictive of depression, being a vulnerability factor as opposed to an outcome (Sowislo & Orth, 2012; Orth, Robins & Roberts, 2008).

To summarise, the Social Risk Hypothesis theorises that depressed mood evolved to aid in avoiding the possibility of social exclusion, during the EEA. Social information is extracted from the world in the domains of agency and affiliation and used to estimate ones Social Value and Social Burden to the group. Combined, these values form one's Social Investment Potential (SIP), which may be experienced phenomenologically as self-esteem. Critically low SIP precipitates an adaptive shift towards a conservative, risk-averse strategy of social investment, experienced as depressed mood.

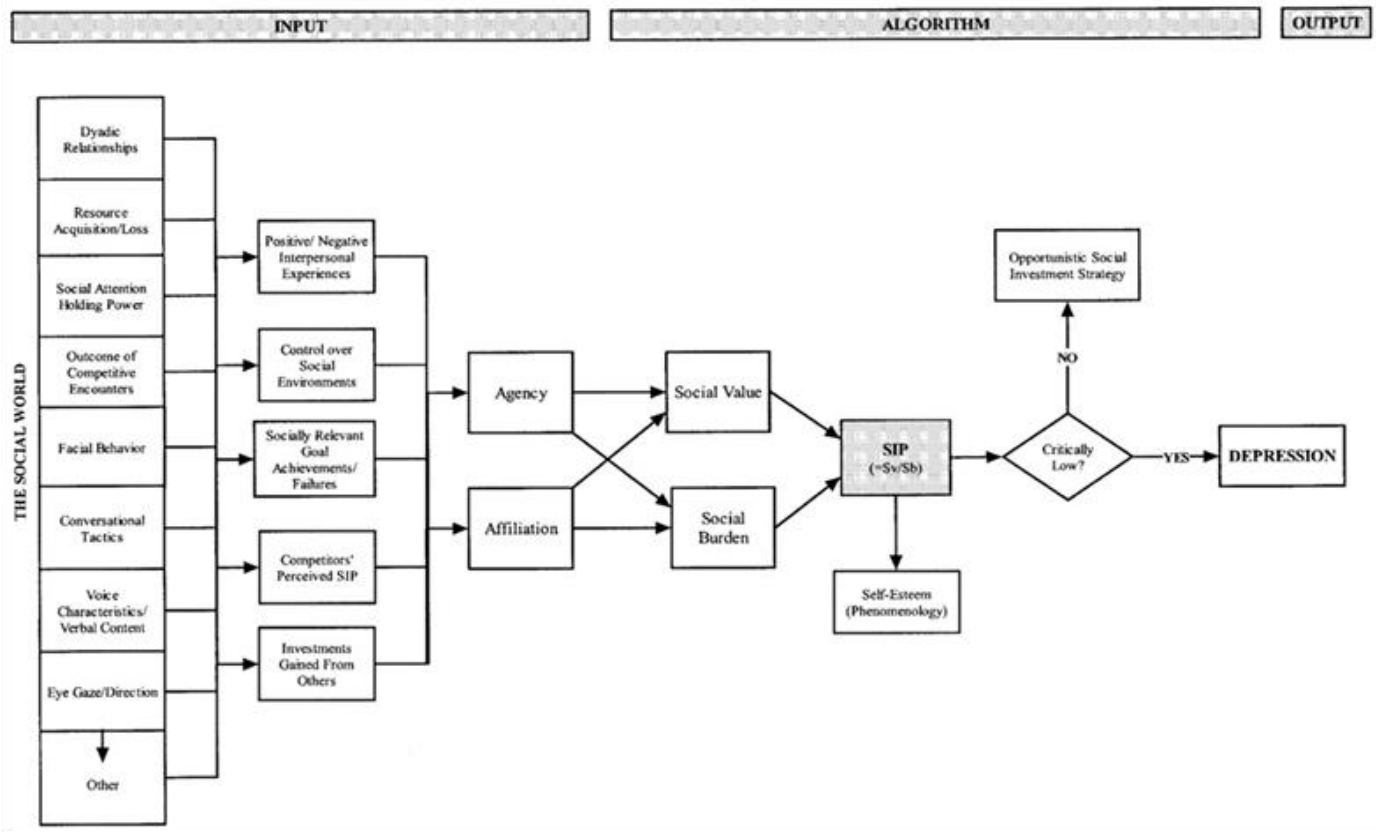


Figure 1.1. Adapted from Allen and Badcock, 2003. Inputs from the Social World contribute to perceptions of Social Investment Potential (SIP). SV; Social Value, SB; Social Burden

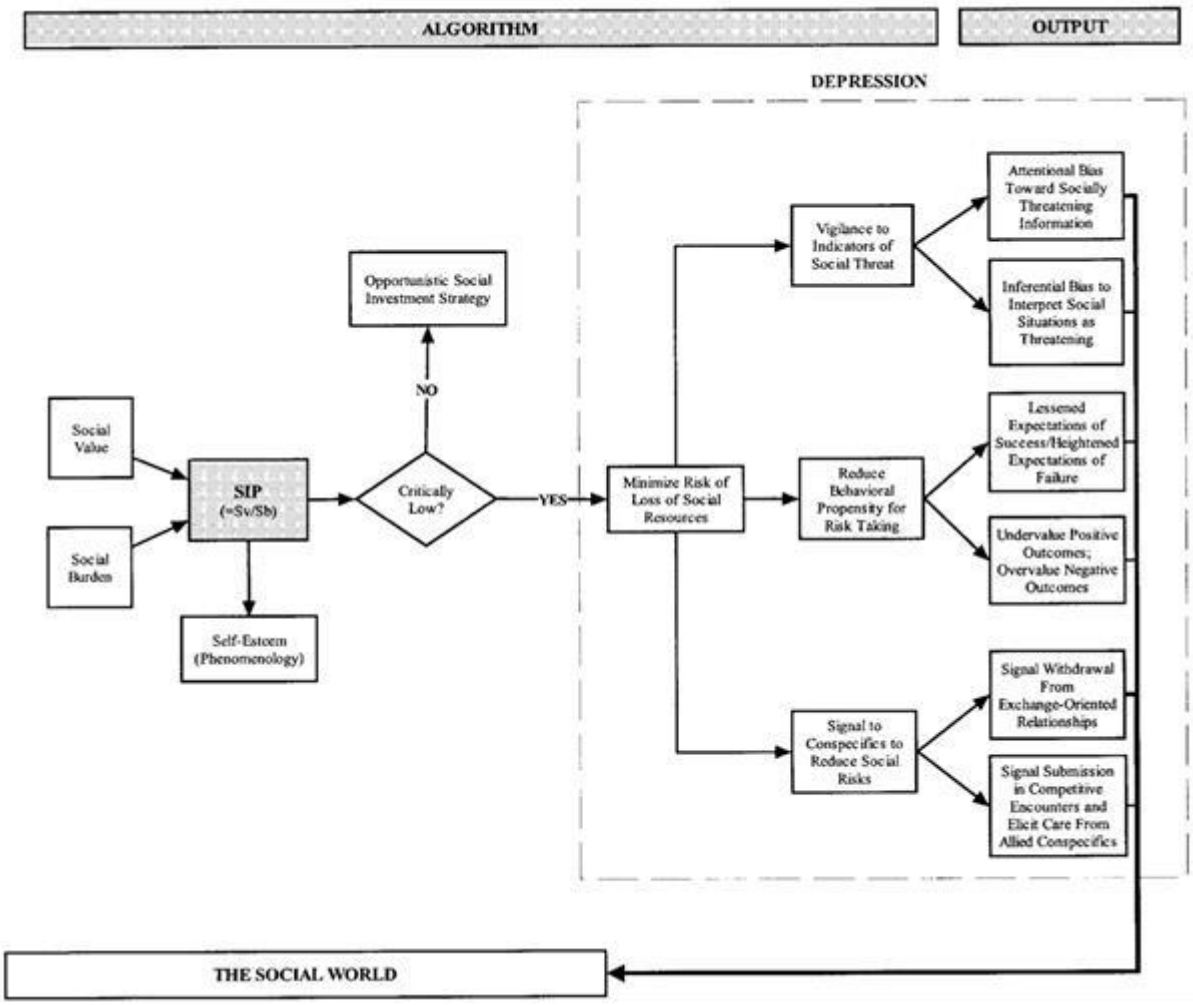


Figure 1.2. Adapted from Allen and Badcock, 2003. Three Key Mechanisms activated by low SIP and their outputs. SIP; Social Investment Potential, SV; Social Value, SB; Social Burden

Mechanisms of Depressed Mood

Allen and Badcock (2003) describe three core mechanisms by which depressed mood functions to improve SIP; hypersensitivity to social risk, communicative signalling to reduce social risks, and reduced social risk taking (Figure 1.2). Hypersensitivity to social risk functions to avoid further reductions in SIP by increasing attention to indications of possible loss. The depressive mechanism achieves this in two ways, firstly by biasing attention towards socially threatening stimuli, and secondly by biasing the inferential rules by which such stimuli are interpreted. In line with this first hypothesis, depressed participants have been found to demonstrate an attentional bias towards socially threatening, as opposed to physically threatening, words (Mathews, Ridgeway & Williamson, 1996) and images (Allen et al., 2001). Similarly, biased vigilance towards subliminal social threat cues has been found to predict greater levels of depressive symptoms (Helzer, Connor-Smith & Reed, 2007), while in healthy subjects, introducing the threat of social exclusion has been associated with an attentional bias towards novel social targets (DeWall, Maner & Rouby, 2009). Importantly, similar attentional patterns are also observed in non-clinical individuals experiencing social isolation (Gardner et al., 2005) illustrating the healthy, adaptive presentation of this bias.

The second component of this mechanism, biasing inferences from social situations, is not intended to increase the accuracy of inferences but rather to “err on the side of caution” by biasing perceptions towards a more negative interpretation. In support of this, Badcock and Allen (2003) found that participants in an induced negative mood state reasoned more adequately about rule violations indicating social risks than neutral participants, and that this ability did not extend to non-social content. There is also evidence to suggest that depressive symptoms are associated with increased perceptions of rejection in social contexts (Andrews et al., 2021; Chen, Liu, Ellis & Zarbatany, 2016; Tabak et al., 2015), and depressed individuals

rate their own performance in social interactions more negatively than controls (Gable & Shean, 2000; Marton et al., 1993). In a specific investigation of interpretation biases, Everaert et al. (2018) had participants complete a Bias Against Disconfirmatory Evidence task (BADE), which involved interpreting unfolding ambiguous social situations. They found severity of depressive symptoms was associated with increased negative and reduced positive interpretation biases, and reduced revision of these interpretations based on disconfirmatory evidence. A daily diary study by Steger and Kashdan (2009) found that depressed individuals reported more instances of negative or unsuccessful social interactions (and feeling a lesser sense of belonging during interactions), and that, compared to controls, their reported level of wellbeing showed greater fluctuations as a result of social interactions.

The second mechanism of action is increased signalling to reduce social threat. Submissive social behaviours are able to elicit signals of care and support from allied conspecifics, and signal defeat or withdrawal in competitive or exchange orientated relationships. This effectively shifts the organism away from high-variance interactions in which the individual might be exploited or defeated, and towards less risky interactions within relationships that are already well-established. This will not lead to large increases in SIP, however, it does provide a more reliable method of eliciting behavioural signals of support. If an individual has too few of these established reciprocal relationships, they will be unable to increase their SIP in this way; this may explain why a lack of perceived social support is associated with severity of depressive symptoms (Rueger et al., 2016; Eldeleklioglu, 2006) while greater perceived social support is associated with measures of resilience (Baltaci, Karatas & Karatas, 2015), and why the social media activity of individuals with depression tends towards a highly clustered and close-knit network of contacts (Choudhury, Counts & Horvitz, 2013).

Such signals might take the form of reduced eye contact (Waxer, 1974), submissive body language (Fisch, Frey & Hirsbrunner, 1983), and fewer positive facial expressions (Girard et al., 2013). Individuals with depression also exhibit many paralinguistic changes including reduced speech volume (Darby et al., 1984), lowered pitch (Talavera et al., 1994), greater hesitancy (Ellgring & Scherer, 1996), less frequent speech (Edison & Adams, 1992), and their voices are more likely to be perceived by others as sad (Tolkmitt, Helfrich, Standke & Scherer, 1982). Signals may also include the content of the speech, for example the tendency to be more self-critical during social interactions, exhibiting greater self-blame and depreciation (Alden, Bieling & Meleshko, 1995). These signals should vary depending on the relational context of the interaction, showing sensitivity to the different risks and opportunities involved. For example, in competitive interactions, individuals with depression respond to perceived dominance in others with exacerbated submissiveness and feelings of inferiority, a reaction that increases with the severity of depressive symptoms (Zuroff, Fournier & Moskowitz, 2007). Meanwhile, sad expressions in kin or friendship interactions elicit automatic approach behaviours (Seidel et al., 2010) and increased generosity (Reed & DeScioli, 2017) in communication partners.

Reduction of Risky Social Behaviours

The third action by which the depressive mechanism operates is through the inhibition of appetitive motivation; this not only reduces an individual's propensity to engage in socially appetitive behaviours, but also acquisitive behaviour towards non-social resources such as food, territory or possessions. This reduces the likelihood of the individual entering into competitive interactions to acquire such resources, and also reduces the individuals' burden on the group by lowering the quantity of non-plentiful resources they require, making them available for others. Lowenstein (2001) posited that emotion influences decision making

processes by affecting our perceptions of value and probability. Allen and Badcock (2003) suggest that in depressed states, the value and probability of losses are overweighted, while those of potential wins are underweighted, leading to a reduction in appetitive and potentially risky behaviours.

Reduced reward responsiveness and lowered positive affect is well documented in depression (Grahek et al., 2019; Germine et al., 2011; Pizzagalli, 2014, Stringaris et al., 2015) while anhedonia, the reduced pleasure or interest in activities, is one of the most common symptoms (Lewinsohn et al., 2003). Theoretically, the purpose of this insensitivity to reward is to reduce the estimated value of rewarding outcomes, thereby reducing the motivation to engage in appetitive behaviours. This has particular relevance to anticipatory pleasure, a specific aspect of motivation linked to desire for reward, as opposed to consummatory pleasure which is linked to satiation (Klein, 1984). Reduced anticipatory pleasure is widely documented in depression (Johnson et al., 2010; Smoski et al., 2011; Dickson & Moberly, 2013; Winch et al., 2015), particularly in the presence of anhedonic symptoms (Pizzagalli et al., 2009). One method of quantifying motivation to acquire rewards is by measuring the effort an individual is willing to expend in their acquisition. Sherdell, Waugh and Gotlib (2012) had participants rate their level of anticipatory and consummatory liking of cartoons, and then engage in effortful tasks in order to view the cartoons. In control subjects, the level of effort a participant was willing to expend was predicted by consummatory liking, while in depressed subjects it was predicted by anticipatory anhedonia. Similarly, in an Effort Expenditure for Rewards Task (EEfRT) Yang et al. (2014) found that severity of depressive symptoms correlated with willingness to expend effort, and that this was predicted by reduced anticipatory pleasure. These findings lend support to the notion that lowered positive affect and reduced reward anticipation is effective in reducing motivation in depression.

Elsewhere, research has linked this reduced motivation to biological mechanisms. Treadway et al. (2012) found in a button-pressing task that participants with depression chose fewer "High Effort" task options than controls. Significantly, the proportion of High Effort choices was positively predicted by the magnitude of dopamine release in the dorsomedial and ventral striatum. Dopamine has been associated previously with incentive motivation and reward seeking (Salamone et al., 2007), and has been found to have lower availability (Klimek et al., 2002) and binding potential (Meyer et al., 2001) in the striatum of individuals with depression. Other literature has utilised the activity of the sympathetic nervous system to quantify levels of motivation in depression. This research is based on the tenets of Motivational Intensity Theory (Brehm & Self, 1989) which conceptualise physiological arousal as the mobilization of resources intended to attain goals. These studies have reliably found that depressed participants exhibit reduced physiological arousal during anticipation of rewards (Brinkmann & Franzen, 2013; Brinkmann et al., 2014; Franzen & Brinkmann, 2015).

Crucially, this reduction in reward and positive affect is associated with lowered risk taking; negative mood inductions have been associated with reduced risk-taking in non-clinical samples (Yuen & Lee, 2003; Clark, Iversen & Goodwin, 2001; Chou, Lee & Ho, 2007) as have sub-clinical depressive symptoms (Kim, Lam, Kutz & Yoon, 2021). As predicted by the SRH, Frey and McCabe (2020) report that elevated uncertainty about social outcomes is linked to reduced motivation to engage in social activities in depressed participants. By comparison, positive mood inductions have been found to increase risk tolerance (Isen & Geva, 1987) and lead to lowered perceptions of risk (Haase & Silbereisen, 2011). Mittal and Ross (1998) found that individuals who received a positive mood induction were more likely to perceive strategic issues as opportunities compared to negative mood participants. Baseline level of positive affect is also associated with taking greater risks (Xiang & Sun, 2011).

Moreover, these changes translate to differences in interpersonal behaviour; positive affect is associated with more confident and assertive interpersonal strategies (Forgas, 2002), while diary studies suggest that levels of positive affect correlate with extraversion (Fleeson, Malanos & Achille, 2002). In comparison, depression is associated with greater levels of shyness (Stewart et al., 2017; Geng et al., 2021). When making interpersonal requests, positive affect is associated with a less polite, more assertive approach, while negative affect is associated with greater caution and more elaborate requests (Forgas, 1999). Similarly, the conversation style of participants in a negative mood complies significantly better with cooperative conversational principles (Koch, Forgas & Matovic, 2013). An interview study from Hamilton et al. (2017) found that trait negative affect was associated with reporting fewer of both positive and negative interpersonal events, while trait positive affect was associated with more of both positive and negative interpersonal events. These findings serve to illustrate that negative affect reduces the occurrence of both SIP increasing and SIP decreasing events, and that changes in motivated interpersonal behaviours may contribute to this effect.

In order to take a risk, we must believe that the potential future outcome is preferable to our current status quo. Reducing the attractive value of future outcomes would therefore be an effective mechanism to reduce risk taking. Examples of this tendency in depressed participants come from studies of delay discounting, where participants choose between a small, immediate reward or a larger reward following a time delay. Depressed participants reliably choose to take smaller immediate rewards, reflecting a lower evaluation of future rewards (Amlung et al., 2019; Caceda, Nemeroff & Harvey, 2014; Pulcu et al., 2014). Given the role of working memory in maintaining reward expectancies (Watanabe, 1996), we might expect disturbances in working memory in depression to be associated with this tendency. Accordingly, Szuhany, MacKenzie and Otto (2018) found that a working memory priming task was able to improve

delay discounting in a depressed sample. Depressed individuals also show blunted activation in neural regions associated with reward expectancy (Chase et al., 2013) and working memory supporting positive future outcomes (Wang et al., 2015).

The above literature focuses on the value placed on rewards, and how this impacts the motivation to acquire them. Another way of reducing propensity for risk-taking is to increase the perceived probability of failure; this may be moderated by our evaluations of our own ability to succeed. Depressive symptoms significantly correlate with lower core self-evaluations (Dunkley & Grilo, 2007; Geng, Li, Han & Gao, 2021) and a tendency to be more self-critical (Deng et al., 2019). Depressed individuals also tend to make social comparisons that are less favourable and more frequent (McCarthy & Morina, 2020; Bazner, Bromer, Hammelstein & Meyer, 2006) which may contribute to a lowered estimation of the likelihood of success in social endeavours. Similarly, believing that one has little control over the outcome of such situations may reduce their attractiveness; Amoura et al. (2014) found that high perception and desire for control was associated with more autonomous motivational styles, while low perception of control was associated with more severe symptoms. Lowered perceptions of control have been observed in depressed samples (Tetrault & Alain, 1999; Senan et al., 2019) and are associated with feelings of helplessness and anhedonia (Seligman, 1974).

In evaluating the likelihood of success, our ability to recall memories of similar events being successful, or to imagine successful outcomes, increases our estimation of such events 35ccurring in the future (Gregory, Cialdini, & Carpenter, 1982). Depression is associated with poorer access to memories of positive, personally relevant events (Gotlib & Joorman, 2010), and rate positive autobiographical memories as less vivid (Werner-Seidler & Moulds, 2010) and less emotionally intense (Werner-Seidler & Moulds, 2012) than controls. Participants with depression also show a specific reduction in the ability to generate mental imagery of positive,

but not negative, future events (Morina et al., 2011; MacLeod & Salaminiou, 2010; Pile & Lau, 2018). Halford et al. (2020) found that depressed individuals described positive personally relevant future events with less specificity, less detail, less imagery and significantly, a lower perceived likelihood of occurring. In contrast, negative autobiographical memories tend to be overgeneralised (Healy & Williams, 1999) and individuals with depression experience intrusive, future-oriented mental imagery of negative events (Holmes et al., 2007; Watson, Berntsen, Kuyken & Watkins, 2012).

Adaptive or Maladaptive

Social Risk Theory (Allen & Badcock, 2003) seeks to explain commonly experienced depressive states that are mild and usually transient, and which represent an adaptive advantage or function. Accordingly, the symptoms addressed within the model are representative of lower levels of depressive severity, including loss of energy (anergia), anhedonia, self-depreciating attitudes, and social withdrawal (Goldberg & Huxley, 1992). Crucially, these are distinct from the clinically significant features of depression, which represent a divergence from the normal function of the adaptive mechanism. Therefore, aspects of the mechanism which are adaptive at the mild to moderate level of severity may become maladaptive in chronic suffers, for example, when protracted signalling to elicit care from conspecifics elicits signals of rejection (Coyne, 1976; Vosk et al., 1982). In the context of the SRH, the development of depression is ascribed to the prolonged failure of the defensive response, causing the individual to enter a dysregulated state outside of the adaptive range (Nesse, 2000). Failure of the depressive mechanism would likely involve chronic low SIP, and has been linked to experiences of entrapment, when the defeating situation which triggered the depressed mood persists or is inescapable. This is supported by the observation that suppression of the flight response commonly pre-dates both depression and self-harm (Gilbert et al., 2002; Clarke et al., 2016),

and the well-established link between chronic stress and depression (Monroe & Hadiyannakis, 2002).

In modern society, many of the fitness enhancing resources that these mechanisms evolved to acquire are no longer reliant on social relationships. Moreover, technological advances have changed not only the structure and stability of our social groups, but the ways in which we interact with others. These changes have the potential to generate new triggers for defensive states, for example encouraging negative social comparisons by artificially inflating the social lives and successes of others (Appel, Gerlach & Crusius, 2016; Alfasi, 2019). Moreover, modern technology interferes with the likelihood that signals of submissiveness will be observed and thereby achieve their adaptive function. These factors may play an important role in understanding why rates of depression have increased in recent decades (Liu et al., 2020).

Some examples of these issues can be seen in recent work exploring the interaction of social media use with symptoms of psychological distress. Social media use has been associated with increased social anxiety, an effect that is mediated by self-esteem (Jiang & Ngien, 2020), as well as reductions in self-esteem (Saiphoo, Halevi & Vahedi, 2020), while limiting social media usage is associated with decreases in feelings of loneliness and depressive symptoms (Hunt et al., 2018). Problematic Social Media Use (PMSU) is defined as excessive concern about social media, a strong drive to use social media, and devoting so much time and effort to social media that it impairs other activities (Andreassen & Pallesen, 2014). PMSU has been associated with increased depressive symptoms (Wegmann et al., 2015; Meena et al., 2012; Koc & Gulyagci, 2013; Hanprathet et al., 2015; Shensa et al., 2017); however, more longitudinal work is needed to establish the directionality of this relationship, and to explore the motivations of excessive social media use.

Evolutionary Systems Theory

More recent evolutionary theories have developed from the over-arching Evolutionary Systems Theory of Psychological Science (EST; Badcock, 2012), a transdisciplinary hierarchical model which is organised around four levels of analysis: functional, phylogenetic, ontogenetic, and mechanistic. We can think of these as organised across increasing levels of variability and explanatory specificity. At the first level, functional explanations are informed by Evolutionary Psychology, which addresses species-typical phenomena. At the second level, Evolutionary Developmental Biology extends evolutionary theory to explain group-level, phylogenetic variability. At the third level, Developmental Psychobiology explains individual-level phenomena produced by ontogenetic mechanisms. Fourth and finally, the subdisciplines of Psychology explain the mechanisms acting in real time, and the consequences of unique environments and developmental contexts.

Importantly, this theory outlines the concept of a hierarchically mechanistic mind (HMM), the idea that psychobiological mechanisms form a hierarchy based on Exclusive processes, which are highly automatic and constrained, extending to Inclusive processes, which are more flexible and able to feed information back into the system. This concept was subsequently developed to integrate the principles of the EST with the Free-Energy Principle (FEP), the theory that biotic organisms actively reduce entropy in their sensory or physical states (Friston, Kilner & Harrison, 2006; Badcock, Friston & Ramstead, 2019). The brain is therefore seen as a prediction generating machine, seeking to optimise our internal representations of the environment through a combination of learning and evolved priors. The adaptive maintenance of the organism's most probable and functional state, such as homeostasis, might then be better conceptualised as an avoidance of unexpected or surprising states. Both perceptual and active processes operate in synergy to minimise surprise and uncertainty.

Previous Free-Energy based theories of depression have posited that a failure to make accurate interoceptive predictions results in sustained physiological stress responses, and that depression represents an attempt to reduce these prediction errors (Seth & Friston, 2016). Others have suggested that depression alters prior expectations of reward, leading to downregulation of reward systems and causing both under-confidence in one's predictions and overweighting the likelihood of social failure (Feldman-Barrett, Quigley & Hamilton, 2016; Joffily & Coricelli, 2013; Moutoussis et al., 2014).

Ancestral social conditions likely required an ability to learn social norms and moderate behaviour contextually, a need which would be well-supported by the flexible, integrated mechanisms of the HMM. Badcock, Davey, Whittle, Allen and Friston (2017) have proposed an Evolutionary Systems Theory of Depression in which risk aversion is an evolved prior, an adaptive response to aversive interpersonal experiences and signals of social volatility. How does this occur? When top-down social predictions are incorrect, the precision of bottom-up social prediction errors increases. This heightens sensitivity to social cues which may provide insight into the cause of the error, reduces confidence in top-down social predictions, and leads to the suspension of goal directed behaviour (anhedonia). Depressive behaviours therefore serve to reduce unpredictability in the social world, through an aversion to risks (events with uncertain outcomes) and alterations in cognition (reduced reward responsivity and hypersensitivity to aversive social stimuli). The sensitivity and precision of bottom-up social prediction errors should be attenuated when these errors resolve, however, depression is precipitated by a failure of sensory attenuation, resulting in attempts to reduce prediction errors by soliciting confirmatory evidence (that social rejection is likely) and ongoing withdrawal from "high-risk" disconfirmatory environments.

Free Energy principles have applicability to understanding emotion more broadly, particularly as predictive coding models are better able to incorporate interoception into explanations of affect (Feldman-Barratt & Simmons, 2015) leading to more unified theories of selfhood, bodily ownership, emotion and perception (Seth, 2013) illustrating the transdiagnostic potential of such theories. Self-perception and the role of embodied cognition in the interpersonal domain is therefore an area of particular interest for ongoing research (Moutoussis et al., 2014).

Discrepancies and Perfectionism

Considering the brain as a generative model which seeks to minimise discrepancies between inputs and expectations may provide insight into the well-established relationship between depression and self-discrepancies (Bruch, Rivet and Laurenti, 2000; Barnett, Moore & Harp, 2017). Self-discrepancies have been conceptualised as triggers for self-regulatory mechanisms (Higgins, 1998; Wells and Matthews, 1984) with the "ideal" self-concept acting as a homeostatic set-point. The suppression of motivated appetitive behaviour in depression might exacerbate symptoms by frustrating the achievement of self-goals, thereby increasing such discrepancies and triggering rumination (Moberly & Watkins, 2010). If we consider discrepancy from a self-imposed set-point as a determining factor in one's experience of social rank, this may provide insight into why individuals who appear stereotypically successful or popular are still at risk of depression (Freeman et al., 2016). Moreover, this might provide insight into the relationship between depression and perfectionism; perfectionism is associated with vulnerability to depression (Cox & Enns, 2003; Melrose, 2011) and social anxiety (Flett & Hewitt, 2014), and subordinate social status is related to higher levels of perfectionism (Wyatt & Gilbert, 1998). Discrepancies are proposed to be particularly salient for perfectionists because they optimise future behaviour (Barke et al., 2017), a goal which would be particularly important for individuals at risk of social exclusion.

Summary

Evolutionary theories of affect provide an integrative approach to understanding disorders such as depression, incorporating social, biological, and functional considerations, allowing us to draw predictions regarding the necessary inputs, mechanisms, and outputs of the condition. Establishing the functionality of such a disorder is key to explaining its etiology, and informs interdisciplinary theories such as EST. Moreover, characterising the positive, adaptive aspects of depressed mood may represent an important shift in how we perceive and diagnose disorders of affect. One of the more influential of these theories is the Social Risk Hypothesis of Depressed Mood (Allen & Badcock, 2003), which proposes that depressed mood evolved to protect an individual from the threat of social exclusion. This is achieved by restoring a favourable ratio of Social Value to Social Burden in a risk averse manner, via three core mechanisms; hypersensitivity to social risk, communicative signalling to reduce social risks, and reduced social risk taking. Together these mechanisms are able to explain many features of non-clinical depressed mood and produce several testable predictions regarding social processing and decision-making. Although many of these predictions have been supported in investigations of memory, attention and response to reward, few studies have explicitly addressed social risk-taking. This thesis is designed to address this gap in the literature.

1.4. NEURAL PROCESSING OF SOCIAL SIGNALS

How then might these changes in social cognition be underpinned at the neural level? Kennedy and Adolphs (2012) describe how the so-called Social Brain arises from widespread activity across many interacting networks (Figure 1.3). While the amygdala network is heavily involved in triggering emotional responses to social cues (Adolphs, 2010), several networks

are responsible for understanding and predicting the behaviour of others; the mirror network through the simulation of observed actions (Keysers & Gazzola, 2007), the empathy network through sharing in others emotions (Vignemont & Singer, 2006), and the mentalizing network by inferring the mental states of others (Dodell-Feder, Koster-Hale, Bedny & Saxe, 2011) (Figure 1.3). Alongside these, activation in the default mode network (DMN), a network of regions typically more active during rest, has also been implicated in social cognition (Mars et al., 2012), as have regions associated with physical pain (Kross et al., 2011) and striatal reward regions (Bhanju & Delgado, 2013). Social perception and behaviour therefore arise from a complex multinetwork system; the precise hypotheses generated by the SRH and EST allow us to create theoretically informed social manipulations, with the goal of identifying a consistent set of implicated regions. The existing literature extends beyond the scope of this thesis, so I will focus on two key mechanisms hypothesised by the SRH, namely hypersensitivity to social rejection and inclusion, and experience of social reward.

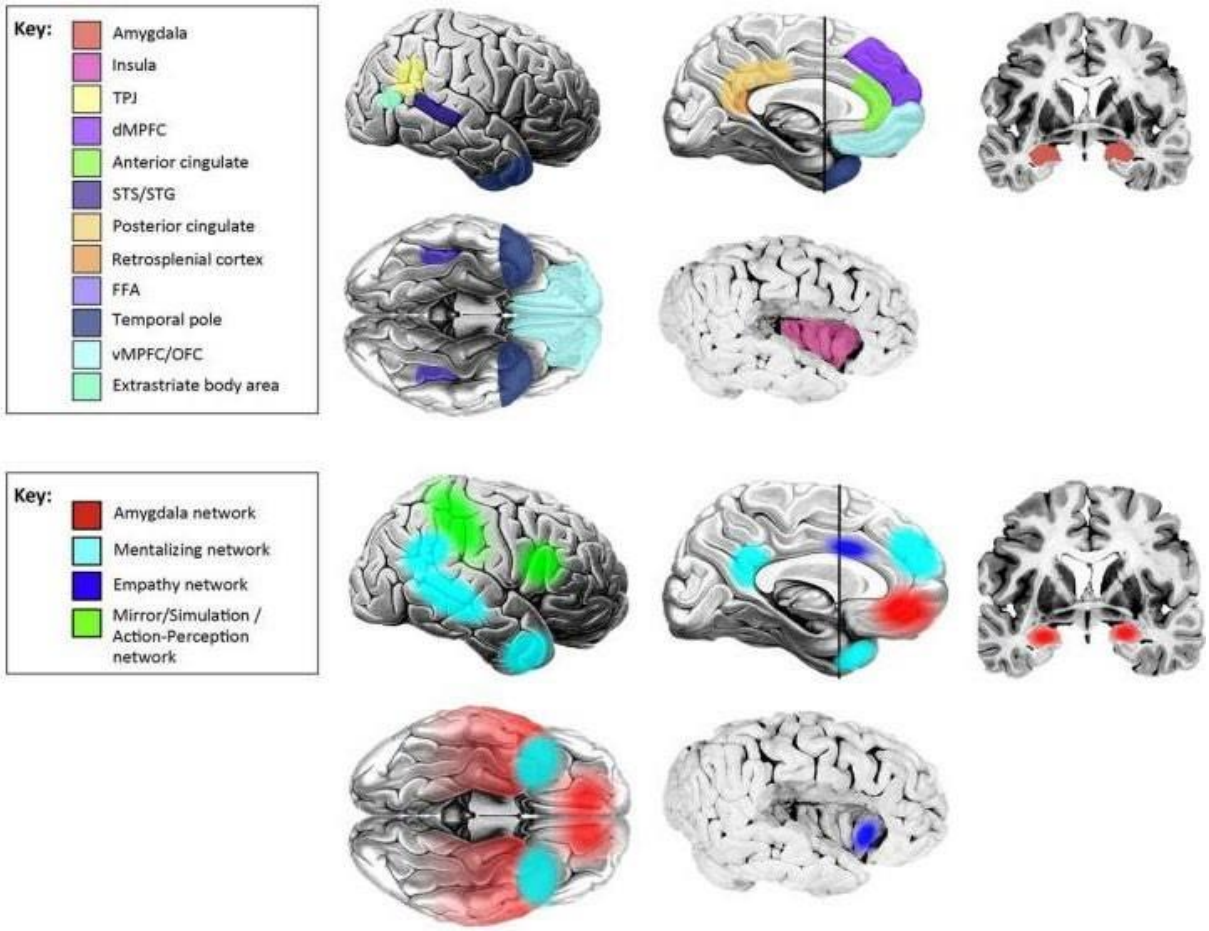


Figure 1.3. Adapted from Kennedy and Adolphs, 2012. The Social Brain: from Structures to Networks. A subset of regions implicated in social processing and four of the key networks they constitute.

Social Rejection and Inclusion

In their seminal paper, Eisenberger, Lieberman and Williams (2003) examined the neural correlates of social rejection during a virtual ball tossing game; their results implicated regions of the anterior cingulate cortex (ACC), typically associated with physical pain, and found these activations correlated positively with self-reported distress. Subsequent research has supported this overlap, finding activation in the dACC when receiving negative social feedback (Somerville, Heatherton & Kelley, 2006), recalling instances of rejection (Najiib et al., 2004)

and watching others suffer social rejection (Beeney et al., 2011). Alongside the dACC, studies of social rejection have frequently implicated the Anterior Insula (AI) (Cheng et al., 2020; Seerhausen et al., 2016) a region also previously associated with physical pain (Lutz et al., 2013), as well as sensitivity to social norms (Xiang, Lohrenz & Montague, 2013; Spitzer et al., 2007).

Given its co-occurring role in conflict-monitoring, previous research characterised the dACC as the brain's "neural alarm-system" (Bush, Luu & Posner, 2000), responsible for detecting and rejecting error signals, with pain being the most primitive trigger for such a system. The overlapping roles of the dACC and AI in both physical and social pain has prompted the suggestion that physical pain processing regions were 'co-opted' during human evolution to increase the salience of social exclusion (Eisenberger, 2012). These regions might then be a viable candidate for the alert system proposed by Sociometer theory (Baumeister and Leary, 1995), which posits that perceptions of rejection or acceptance are integrated into self-esteem, acting as a warning of potential exclusion. In support of this, Eisenberger, Inagaki, Muscatell, Byrne-Haltom and Leary (2011) found that greater activation in the AI and dACC during negative social feedback was associated with lower ratings of self-esteem. More recent findings have supported the involvement of this region tin processing signals of social inclusion; a study in healthy adolescents found comparable dACC and AI activation in response to both positive and negatively valenced social feedback (Dalgleish et al., 2017) providing promising evidence for a shared neural circuitry.

As noted above, the SRH predicts heightened interpersonal sensitivity in depressed mood, particularly in response to signals of social risk. Accordingly, depressed individuals have been found to exhibit greater activation in response to social rejection in both the AI and dACC (Yttregahl et al., 2018; Silk et al., 2013; Dedovich, Slavich, Muscatell, Irwin & Eisenberger,

2016), and significantly, similar patterns of sensitivity have been observed in individuals with low self-esteem (Schie et al., 2018; Onoda et al., 2010). Eisenberger and Lieberman (2004) discuss how an effective alarm system requires capabilities of both discrepancy-detection and "alerting". The overlapping roles of the dACC-AI in processing of social expectancy violations and negative affect would appear to fulfil both requirements and have similarly prompted some authors to suggest that emotions might be underwritten by their own error signals, used to "direct the organism to zero", that is, to motivate us towards a homeostatic state (Montague & Lohrenz, 2007). Moreover, embodied interactions may contribute to the mentalization of one's physiological self and interoceptive states, also aiding in homeostatic processes (Fotopoulou & Tsakiris, 2016). It may be valuable for future research to consider this in the context of Evolutionary Systems Theory, in which motivated reduction of entropy is a central tenet.

There is currently much debate in this literature regarding to what extent subregions of the dACC and insula either process expectancy violation or affect. Many previous studies of social rejection utilised a version of the Cyberball paradigm (Williams, Cheung & Choi, 2000) in which social exclusion is compared against an "inclusion" condition in which all participants are included equally (Vijayakumar, Cheng & Pfeifer, 2017), meaning the social exclusion condition represents a greater violation of social norms than the inclusion condition (Somerville, Heatherton & Kelley, 2006). Kawamoto et al. (2012) addressed this utilising a protocol with an overinclusion condition, finding that the dACC was more activated by exclusion relative to overinclusion, in support of social pain accounts. However, in a similar protocol, Cheng et al (2020) found a more complex picture; dACC and posterior insula activity was found to increase with exclusion and decrease with overinclusion, and dACC activity correlated with reported affective distress, however, the dACC and AI also responded to events which violated short term expectancies. A recent review of the literature from Krueger et al.

(2020) proposed that the ventral region of the AI represents 'violations of expected outcomes' which trigger inequality related negative emotions, whereas the dorsal region represents 'violations of expected intentional behaviour', which relates more to social processes such as betrayal or punishment.

Social Reward

The SRH posits that reduced socially appetitive behaviours in depression may result from the lowered experience of reward from interpersonal interactions. Hypo-functioning of the Nucleus Accumbens (NAcc) in depression has been associated with this reduced social reward processing (Laurent & Ablow, 2012; Kupferberg et al., 2016; Nusslock & Alloy, 2017; Rey et al., 2009). The NAcc forms part of a network of regions believed to be involved in social affiliation and reward, spanning the rostral and subgenual regions of the anterior cingulate cortex, ventromedial PFC and striatum, dorsomedial temporal pole and entorhinal cortex (Bickart et al., 2014). The NAcc is connected to several neural regions which might modulate its activity, including the anterior insula (Cartmel, Chun & Vickery, 2014) and PFC (Vialou et al., 2014) which have been found to modulate social avoidance behaviours in mice models. The reduced experience of social reward in depression might also be traced to lowered attributions of salience towards positive social information, evidenced in hypoactivation of the amygdala in response to socially rewarding stimuli (Stuhrmann et al., 2013; Dernt et al., 2011). Lastly, depressed individuals show structural and functional alterations across many of the widely distributed regions implicated in the default mode network (DMN), and its involvement in social function (See review from Cusi et al., 2012). With relevance to social reward, Crawford, Muhlert, MacDonald and Lawrence (2020) investigated the relationship between regional grey matter volume (rGMV) and expectations of social acceptance orrejection, finding that increased rGMV in DMN regions including the ventromedial prefrontal

cortex correlated with higher social reward and lower social threat expectancy. By comparison, social threat expectancy correlated with rGMV in regions associated with interoception (somatosensory cortex) and social attention (posterior superior temporal sulcus).

Summary

Depression is associated with disturbances in activation across several widespread networks involved in social function. Relevant to this thesis, diminished reward-system activation may underlie reduced attributions of salience to positively rewarding social stimuli, resulting in lowered motivation to initiate social interaction or competition. Research attempting to elaborate a coherent neural system for the monitoring of social rank and inclusion is still ongoing, and presently involves a complex mix of regions subserving social and physical pain alongside prediction-error and interoception. As yet, much of this research has not yet adequately considered depression, despite the widespread alterations in social function. Understanding how these regions respond to social signals and discrepancies in depressed individuals may be valuable, not only for our interpretation of this condition, but also for placing it within a wider evolutionary theory of socio-affective mechanisms.

1.5. NEUROECONOMIC GAMES

Everyday social behaviour involves a range of complex perceptual and behavioural functions, including integration of contextual information, understanding and inferring the beliefs of others, and the application of appropriate interpersonal strategies. We have seen in this chapter how these functions are disrupted at both the behavioural and neural level in depression (Kupferberg et al., 2016) and other psychopathologies (Panchal, Kaltenboeck & Harmer, 2019), representing a transdiagnostic deficit that has relevance for understanding the etiology

of affective disorders. However, operationalising and assessing such varied behaviours presents significant challenges to both cognitive researchers and clinicians; neuroeconomic games provide an informative framework to do so.

Game Theory paradigms mimic real-life, dynamic social interactions, allowing social decision-making to be studied under controlled laboratory settings (Robson et al., 2020). A subgroup of these paradigms, neuroeconomic games, integrates neuroscience, psychology and economics, providing a quantifiable method for evaluating these behaviours in normative and psychiatric populations. Such paradigms allow mathematical depictions of interpersonal behaviours,which can be utilised in developing mechanistic accounts of dynamic social behaviour and social signalling (Camerer, 2008). Importantly, this approach is transdiagnostic; King-Casas and Chiu (2012) describe how multi-agent economic games comprise measurement of three discriminating social vectors, including social valuation, social risk preferences, and social inference, which underlie a range of psychiatric illnesses (Figure 1.4). More recently, Robson et al. (2020) related this to dimensions of the Research Domain Criteria (RDoC) Affiliation and Attachment, Reward Responsiveness, Reward Learning and Reward Valuation. Additionally, these games have translational value as a quantifiable method of evaluating interpersonal treatment outcomes (Kirk, Downer & Montague, 2011). This thesis utilises two neuroeconomic games, the Ultimatum Game, and a Public Goods Game to explore social decision-making and risk behaviour in depression.

interpersonal decision-making	social inference	social valuation	social risk preferences
atypical interpersonal functioning	• theory of mind deficits • instrumental aggression	• increased or decreased interest in social activities • irritability toward social partners	• anxiety specific to social evaluation • paranoia about social partners
examples in psychiatric illness	• social impairments in autism spectrum disorders • psychopathic traits in antisocial personality disorder	• impulsive social behavior in mania • social anhedonia in depression • peer influence in substance use	• social phobia • distrust in borderline personality disorder • paranoia in psychotic disorders • aggression in PTSD

Figure 1.4. Adapted from King-Casas and Chiu, 2012. Core dimensions of social decision-making addressed by neuroeconomic games, and their relevance to psychiatric illness.

The Ultimatum Game

The Ultimatum Game (Guth et al., 1982) is a well-established neuroeconomic game involving two players; a Proposer, who is endowed with a sum of money, and a Responder. The Proposer decides how much of their sum they would like to offer the Responder. If the Responder accepts the offer, the money is divided according to the proposed split, however, if the Responder rejects the offer, neither player receives anything. Theories of utility maximisation predict that the Proposer should offer the minimum possible sum, and the Responder should accept any offer above zero (Rubinstein, 1982); however, traditional findings indicate that Proposers offer between 30-50% of their stake, and Responders reject offers below 30% (Camerer & Fehr, 2004). These patterns are extremely consistent amongst classic studies of the UG (Guth and Kocher, 2013). There are several theories as to why these behavioural patterns emerge, and many models of the behaviour; a review from Debove and colleagues (2011) cited 36 models, falling into six categories, based on empathy, reputation, spite, noise, spatial-population-

structure and alternating-roles. Several of these models converge around the importance of enforcing social norms, and the variously rewarding experiences of fair and unfair treatment. Humans have a strong sense of reciprocity; they will punish individuals who attempt to exploit their group, even when there is no personal benefit to them (Boyd et al., 2003) or when there is a cost (Fehr & Gachter, 2000). This may be rooted in an inherent sense of justice (Tyler, 1991), evolved from the adaptive advantages that are gleaned from a cohesive social group (Silk, 2007). Making fair offers and rejecting unfair offers may then reflect our need to enforce these norms (Fehr, Fischbacher & Gachter, 2002). Rejection of unfair offers is therefore often characterised as a form of altruism because it enforces the social fairness norm, at a loss for the Responder (Fehr & Gachter, 2002). This is especially true in one-shot (single round) versions of the game, where the Responder cannot hope to benefit from enforcing this norm (Fehr & Fischbacher, 2003).

However, these theories of reciprocity are not universally accepted; Wells & Rand (2012) performed a modified UG in which they removed any prosocial motivations; the payoff of the Responder was a fixed value, regardless of whether they accepted or rejected the Proposer's offer. Therefore, the only reason to make an offer above zero was a strategic desire to avoid rejection. The authors found no significant difference in offers between this version of the game and a classic UG, and concluded that a self-interested desire to avoid rejection was enough to explain traditional findings. Yamagashi et al. (2012) conducted a range of neuroeconomic tasks including the Ultimatum Game, Dictator Game, Prisoner's Dilemma and Trust Game. They found no correlation between participants' rejection of unfair offers and prosocial behaviour in subsequent tasks, leading them to conclude that rejection of unfair offers is more indicative of a desire to avoid accepting an inferior status relative to the Proposer.

Some insight into possible motivations can be gained from considering the size of the stake. Theories of human reciprocity emphasize the importance of the intentionality of an action over its material outcome (Falk & Fischbacher, 2006). This explains why receiving fair treatment leads to positive emotions even when the absolute material outcome is controlled (De Cremer & Alberts, 2004), because the salient factor is the implied social acceptance, another basic human motivation (Baumeister & Leary, 1995). Traditional behavioural findings agreed that stake size was of little relevance; in Cameron's (1999) study in Yogyakarta, Indonesia, participants played for sums equivalent to up to three months' salary, finding that Responders were just as willing to reject unfair offers, and Proposers made slightly less selfish offers as the stakes increased. Similarly, Slonim and Roth (1998) reported changes in stakes had only a small effect on play, even when the financial stakes were varied by a factor of 25 (although they observed that when participants played over extended periods, high stakes proposals showed a small decline). Recent literature, however, has reported a larger effect of stake; Anderson et al. (2011) varied stakes by a factor of 1000, and found a significant effect of stake size among Responders. Novakova and Flegr (2013) varied stakes even further using a hypothetical questionnaire version of the UG, allowing them to pose stakes between $1-$10,000, and found a significant relationship between the amount at stake and the minimum acceptable offer. These more recent findings indicate that enforcing social norms may become too costly at a certain point, however, as Novakova and Flegr reflect, that point is very high.

Public Goods Games

Public Goods Games (PGGs) allow the observation of cooperative group behaviours in the presence of an incentive to defect. Players are endowed with a sum of tokens with a designated monetary value. In each round, players choose how many tokens to keep in their individual account, and how many to contribute to a group pot which will be multiplied and split equally

amongst the players. The group as a whole will gain the most resources if everyone contributes their total endowment in each round, thereby maximising the number of tokens multiplied. However, an individual can earn more, and minimise their own risk of loss, by contributing nothing and keeping their endowment in addition to their share of the pot (Olson, 2009). This strategy has been termed "Freeriding", and Nash Equilibrium models predict that this should be the dominant strategy in inherently self-interested beings.

However, traditional findings present a challenge to these assumptions; individuals tend to contribute far more than the minimal levels predicted (Ledyard, 1995) with the most prevalent strategy type being one in which players contributions are directly correlated with their beliefs about the contributions of others, termed the "conditional co-operator" (Kurzban & Hauser, 2005; Keser & van Winden, 2000). This has led to the emergence of theories of cooperation based on a need for reciprocity (Rabin, 1993) and a negative emotional response to inequity (Bolton & Ockenfels, 2000). While these cooperative behaviours tend to decrease over the course of the game (Chauhuri, 2011) this decline can be addressed by including the option to punish non-cooperators (Balliet, Mulder & Lange, 2011), indicating that a combination of pro-social and self-protective mechanisms may be at work. PGGs uniquely allow us to investigate these behaviours in a group setting, which has found that participants tend to be most cooperative in groups of similar individuals (Gachter & Thoni, 2005) or in the presence of an out-group threat (Tan & Bolle, 2007).

The PGG paradigm allows us to observe how much of their resources an individual is willing to risk in order to avoid being a burden to the group (a Freerider), which may reflect behavioural tendencies designed to rebalance ones perceived SIP. Moreover, the inclusion of a punishment element allows us to test predictions regarding social punishment sensitivity and negative affect.

Neuroeconomic Games in Affective Science

Studies involving the UG report that individuals with depression make more generous offers than controls (Scheele et al., 2013; Destoop et al., 2012), but surprisingly, tend to reject unfair offers at a higher rate, resulting in losses for both themselves and the Proposer (Hinterbuchinger, 2017). By comparison, individuals with Generalised Anxiety Disorder tend to accept unfair offers more frequently than controls and perceive such offers as less unfair (Grecucci et al., 2013). These findings may reflect differences in the level of negative affect experienced by these groups following perceived unfair treatment (Paz et al., 2017). Notably, in depressed samples, rejection of unfair offers correlates positively with the severity of depressive symptoms (Wang et al., 2014) and is not typically observed in non-clinical or moderate samples (Pulcu et al., 2015) and may therefore be indicative of maladaptive presentations of depression. Individuals with schizophrenia behave in a less financially strategic manner compared to controls in the game (Billeke & Aboitiz, 2013), tending to make more hyper-fair offers (Agay et al., 2008; Wout & Sanfey, 2011), accept more unfair offers (Csukly et al., 2011) and reject more fair offers (Yang et al., 2017). Rejection of fair offers has been attributed to low self-esteem, perhaps causing a feeling of “not deserving” a fair share (Robson et al., 2020), and to impaired Theory of Mind (ToM) and suspiciousness, causing misunderstanding of the Proposer’s intentions (Wischniewski & Brune, 2011). This latter explanation might be supported by findings that individuals with Autism Spectrum Disorders (ASDs) exhibit the same pattern of behaviour, rejecting more fair offers and accepting more unfair offers (Sally & Hill, 2006), a pattern that has also been attributed to difficulties interpreting the intent of the Proposer.

Currently, research utilising the PGG within clinical samples is very limited, however, some insight can be derived from literature involving the Prisoners’ Dilemma, which also assesses

cooperation albeit in a two-person scenario. This literature currently yields conflicting results, in both subclinical and depressed participants, reporting less cooperation (Clark et al., 2013; Pulcu et al., 2015) and more cooperation (Sorgi & Wout, 2016), while research in GAD samples has produced similarly mixed results (McClure et al, 2007; McClure-Tone et al., 2011). Consistent with findings elsewhere in the neuroeconomic literature, these studies reportpatients experiencing more negative emotional responses to betrayal or non-reciprocal treatment compared to controls (Haley & Strickland, 1986; McClure-Tone et al., 2011). Interestingly, there is evidence that both depression (Sorgi & Wout, 2016) and GAD (McCluree t al., 2007) are associated with greater sensitivity towards a partner's contribution style; patients show greater generosity than controls when their partner is cooperative but behave lesspredictably and, in some cases, less cooperatively when the partner defects. One possible characterisation of these findings might be that, while patients initially demonstrate increased cooperative tendencies, poor emotional regulation in response to negative interpersonal experiences disrupts this pattern, leading to withdrawal of resources from situations where thepartner is seen as unreliable.

Although not utilised in the current protocol, The Trust Game (Berg et al., 1995) has also been used to investigate fairness and reciprocity. In this game, participants play the role of either the Investor or the Trustee. The Investor chooses what proportion of their money they would like to send to the Trustee, this sum is then multiplied, and the Trustee decides how much they would like to send back. Remitted depressed individuals have been found to show greater levels of reciprocity in this game than never-depressed participants (Zaki & Gruber, 2017) and suicidal ideation has also been associated with increased reciprocity in the game (Caceda et al., 2014). This paradigm creates the opportunity to defect or 'cheat' by sending back a less than equal share, especially in versions where the full multiplied sum is not revealed to the Investor.

Depressed participants typically cheat less than controls in this game (Zhang, Sun & Lee, 2012), and studies which have manipulated the risk of being caught cheating find that this reluctance to cheat is stable even when the risk of detection is low (Shao et al., 2015). Individuals with Bipolar Disorder also exhibit higher levels of reciprocity in this game (Ong, Zaki & Gruber, 2017) while patterns of reduced trust and abnormal TPJ activation during the game have been observed in both posttraumatic stress disorder (PTSD) (Cisler et al., 2015) and psychosis (Gromann et al., 2013).

Summary

Overall, neuroeconomic games represent a promising set of paradigms for quantifying social behaviours and elucidating their underlying mechanisms, with applicability to transdiagnostic research and theory. In the current thesis, these games are utilised to investigate social risk taking, in the context of the Social Risk Hypothesis of Depressed Mood. Previous use of neuroeconomic games in depressed samples finds evidence of increased reciprocity and more generous contribution patterns (Zhang, Sun & Lee, 2012; Scheele et al., 2013). This type of prosocial behaviour might be interpreted as a way to maximise one's social value, or may be evidence of hyper-altrusim (Kaufman & Jauk, 2020). However, these interpretations need to be reconciled with concurrent findings of low cooperation (Clark et al., 2013) and rejection of offers in the UG (Hinterbuchinger, 2017). These behaviours might result from deficits in executive function causing difficulties in strategy-switching (Must et al., 2006), or from poor regulation of negative emotional responses leading to disengagement of attention (Gradin et al., 2015). In this thesis, we will discuss these patterns in more detail and consider whether superficially anti-social behaviours might in-fact reflect an altruistic tendency to enforce social norms.

1.6. SUMMARY AND AIMS

Depression is a widespread and debilitating condition associated with disruption to social functioning. Evolutionary theories of depression provide an integrative approach to understanding the etiology and mechanism of the disorder and have implications for broader theories of affect. The Social Risk Hypothesis (Allen & Badcock, 2003) posits that depressed mood functions to reduce the risk of social exclusion via three key mechanisms; hypersensitivity to social risk, communicative signalling to reduce social risks, and reduced social risk taking. In depression these mechanisms act outside the range of adaptive functionality, however, the organisation of the mechanism remains the same, making this an appropriate population in which to observe the inputs, outputs and transformations predicted by the model. Current research has failed to address one of the core features of this mechanism, the reduction of risky social behaviours, which is subserved by psychological processes which alter perceptions of social risk to overweight the likelihood and magnitude of loss, impacting self-esteem. Neuroeconomic games present an opportunity to examine such a strategy during dynamic social interactions, providing a more ecological paradigm than in previous literature.

A key focus of previous research regarding depression is within the domain of affective processing, however, interest in socio-affective processing is still gaining pace. Existing evidence has indicated altered social function in depression, indicating that this area warrants further research. Moreover, the observation of similar difficulties across affective disorders indicates that these functions could play a key role in transdiagnostic practice, and in interdisciplinary theories of psychological processes. Homeostatic and Evolutionary Systems approaches have theorised that these functions may be underpinned by the goal of reducing entropy in one’s environment, which highlights the importance of understanding how discrepancies are perceived and responded to.

The work in this thesis therefore aims to expand our understanding of social processing in depression within a socio-evolutionary framework. Firstly, this thesis will investigate how social and self-discrepancies are processed at the neural level, to better characterise the role of the dACC/AI, and draw comparisons between depressed and control samples with relevance to the SRH and homeostatic theories of affect. Secondly, this thesis will examine the behavioural predictions of these theories, with emphasis on addressing the previously under-researched concept of social risk-taking, and will improve on methodological issues in previous investigations of social function, utilising novel social adaptations of behavioural measures and a group-induction design.

CHAPTER 2. PROCESSING SOCIAL DISCREPANCIES: REANALYSIS OF AN EXISTING DATASET

2.1. INTRODUCTION

The socio-evolutionary theories discussed in Chapter 1 characterise affect as part of a system of perceptual and behavioural mechanisms which serve to rectify survival relevant discrepancies. The Social Risk Hypothesis of Depressed Mood (SRH; Allen & Badcock, 2003) characterises depressed mood as one such mechanism, which is triggered by discrepancies from a social set-point, an individual homeostatic ideal where one's social value versus burden are at their optimum ratio. At this point, it is valuable to distinguish two relevant forms of discrepancy; between our actual and ideal self-concepts (intrapersonal), and between our own views of our actual (and indeed, ideal) selves and the judgements of others (interpersonal). An intrapersonal discrepancy might indicate the need to engage corrective mechanisms to move oneself closer to the "set-point", while an interpersonal discrepancy might additionally indicate the need to update one's self-concept or seek to change others' views of oneself. The neural correlates of both remain largely unexplored; this chapter examines interpersonal discrepancies by reanalysing behavioural and neuroimaging data acquired from a social feedback task, described in Dalgleish et al., (2017), in which participants made videos about themselves and subsequently received feedback on the videos from 'expert raters', placing them in one of four ranked positions. This reanalysis aims to 1) investigate whether discrepancies between our self-perception and the social-rank feedback we receive are processed distinctly from absolute feedback type, and 2) identify trait factors which might interact with this processing. In the context of the thesis, this chapter provides insight into the neural signature by which homeostatic affective mechanisms might be triggered, and informs subsequent investigation of these concepts in Chapters 4 and 5.

Perception of Self-Discrepancy and Affective Disorders

Self-Discrepancy theory proposes that humans possess a multiplicity of self-concepts; an ideal self, based on our ultimate goals, an ought self, based on our responsibilities and feelings of obligation, and an actual self, which represents how we believe ourselves to be in reality (Higgins & Higgins, 1987). Discrepancies between the ideal-self and actual-self have been repeatedly associated with depressive symptoms (Johns & Peters, 2012; Strauman, 1989) and are predictive of depression over a 3-year follow-up period (Watson, Bryan & Thrash, 2016). Moreover, self-discrepancies show significant test-retest reliability over time, possibly therefore being representative of a stable trait (Watson, Bryan & Thrash, 2016). Distinguishing the concept of actual-ideal discrepancy "from the person's own standpoint" and "from the perceived viewpoint of others" finds that own-perspective self-discrepancies are the most consistent predictor of specific affective states, being negatively associated with joviality, self-assurance and surprise, and positively associated with sadness, while feelings of guilt and reduced serenity are associated with self-discrepancy from the perceived view of others (Barnett, Moore & Harp, 2017).

Little neuroimaging research has specifically investigated discrepant social feedback, however, there is literature regarding *unexpected* social feedback; An EEG study from Molen et al (2017) found that unexpected social rejection elicited more activation in the dorsal anterior cingulate cortex (dACC), insula and inferior frontal gyrus compared to expected rejection. Thesefindings align with the role of the dACC in the coding of prediction error (Bush, Luu & Posner,2000) and indicate its involvement in the violation of social expectancies. In Chapter 1, we discussed how the dACC has been proposed as a key candidate region for a neural "Sociometer", a system which integrates signals of rejection and inclusion to monitor one's social rank (Eisenberger et al., 2011). With regard to self-discrepancies, neuroimaging researchfinds that reflecting on large actual-ideal self-discrepancies is associated with increased activity

in the dorsal medial prefrontal cortex (dMPFC) and dorsal striatum (Shi et al., 2016). As the dMPFC has been implicated in the down-regulation of emotion responses during craving (Kober et al., 2010), the authors proposed that it might also be downregulating emotion responses to a large self-discrepancy. Interestingly, individuals with lower self-esteem have been shown to have lower dMPFC activity in trials of negative low-relevance words (Yang, 2014). Given that this was specific to words of low personal relevance to the individual, this finding could be seen as supporting the conclusion that dMPFC protectively downregulates emotional responses to certain feedback, and that a failure to do this may contribute to low self-regard (Shi et al., 2016).

Separating self-discrepancy and expectancy-violation

When considering discrepant feedback, a possible confound is the effect of expectancy violation. Dalgleish et al. (2017) investigated neural activation associated with receiving positive, negative and neutral social-rank feedback; participants were asked to make videos about themselves, which they were told would be judged by a trained expert in relation to three other participants. Participants then viewed their ratings during a scanning session. Activations common to both positive and negative feedback were observed in the dACC and AI. As the dACC has been associated with prediction-error processing (Botvinick, Cohen, & Carter, 2004), Dalgleish et al. (2017) performed a sub-analysis to demonstrate that its activation in their study was driven by social feedback and not expectancy violation. They examined a sub-group of participants who had consistently rated themselves as superior to other participants across all characteristics (n=10); for these individuals, positive feedback was expected and therefore activation during positive trials could not be attributed to expectancy violation. In support of their conclusions, they found that the dACC region remained significantly active during positive feedback but not during negative feedback. This finding is similar to that of a

previous study by Kawamoto et al., (2012) which found that the dACC was specifically associated with social-feedback, regardless of expected outcomes.

Aims of the current reanalysis

Social Feedback communicating a discrepancy from one's actual or ideal self-perceptions may constitute an important trigger for homeostatic affective and behavioural mechanisms. Despite this, neuroimaging research attempting to isolate neural regions associated with discrepancy is lacking. This chapter aims to use secondary data analysis to 1) identify whether there are specific neural regions for the processing of discrepancies between our self-perception and social-rank feedback, and 2) to investigate possible trait factors which might interact with this processing.

2.2. METHODS

The methods of data collection were previously reported in Dalgleish et al. (2017), from whom these data were acquired. Participants were 60 adolescents (Mean age=18, range 17-20, 31 female) recruited from the ROOTS cohort (Lewis, Jones & Goodyer, 2016). Three participants were excluded from further analysis after reporting disbelief in the study cover story, and one due to failure in imaging acquisition, resulting in a total of 56 participants. Inclusion criteria were normal or corrected-to-normal vision and being English speaking. Exclusion criteria were history of neurological trauma, current neurological disorder or Axis 1 psychiatric disorder according to the DSM, specific learning disability, IQ<85 on the Wechsler Abbreviated Scale of Intelligence, current use of psychotropic medication, or presence of metal in body.

Social Feedback Task

In this paradigm, participants were told that they would compete with three other participants, located at other brain scanning facilities in the UK (hyperscanning), to impress a panel of six judges and thereby win through three rounds of tasks. In fact, there was only ever one round, with the participant being "voted off" at the end of this round, and the judges and other participants were stooges. For the first (and only) round, participants made a one-minute video recording about themselves, for example detailing their aims and achievements or what was important to them in life. They were told that these videos would be rated for six socially relevant characteristics that had been reliably linked to social success; social competence, motivation, self-confidence, personal strength, social attractiveness & emotional sensitivity. Ratings would be assigned by the six judges, gathered in a separate location, who had been extensively trained in making social judgements from such recordings. They were told that each judge would rank all four participants (in fact, one participant and three stooges) from best to worst on each attribute, resulting in 36 sets of feedback per participant, and these ratings would determine who proceeded to subsequent rounds. To improve believability participants also rated themselves and the other participants for each of the 6 attributes on a scale of 1-10.

Participants viewed the judge's ratings of them in the scanner. Each judgement epoch comprised three components separated by fixation periods. First, an 8-second 'Judge Slide' detailing which judge would be rating which attribute. There was then an 8-second fixation period before the 8-second 'Feedback Slide' which showed where the participant had been ranked relative to the other three participants. There was then a 2-second fixation period before the final 10-second 'Rating Slide', where participants rated how they felt about the feedback from 0 (disappointed) – 10 (pleased). Over the 36 judgement epochs each participant received 12 top rankings, 12 middle rankings and 12 lowest rankings. After all judgements were made participants saw each judge's final judgement determining whether they would continue to the

next round, resulting in their being rejected from subsequent rounds. Following scanning, participants were asked a series of questions to assess their acceptance of the task story.

Questionnaires

Two questionnaire measures were included in the current analysis. The Cognitive Emotion Regulation Questionnaire (CERQ; Garnefski, Kraaji & Spinhoven, 2001) is a self-report measure which assesses 9 cognitive strategies of emotion regulation across 36 items. The measure has good factorial validity and reliability (Garnefski & Kraaij, 2007) and is suitable for individuals aged 12 years and older. The Behavioural Inhibition and Approach Scale (BIS/BAS; Carver & White, 1994), is a 24 item self-report measure based on Gray's (1982) two general motivation systems, inhibition and activation. The current analysis included two of the questionnaire's four subscales; the behavioural Inhibition Scale (BIS), which measures concern over the possibility of negative events and sensitivity to those events, and the Reward Responsiveness subscale of the Behavioural Activation Scale (BAS), which measures sensitivity to reward. Previous literature has found the BIS relates to measures of neuroticism and negative affect, while the BAS relates to positive affect and extraversion (Jorm et al., 1998).

Reconfiguring to address discrepancy

For this reanalysis it was first necessary to establish where participants expected they would rank in relation to the other three participants for each of the 6 judged characteristics. This was calculated using participants 1-10 ratings of themselves and the other participants for each attribute. Their ratings of the others were averaged, and their own self-rating was then subtracted from this value; this gave a single 'Expectancy value' indicating whether they expected to rank higher or lower than the others for that characteristic (with more negative

values indicating they expected others to do worse, and more positive values indicating they expected others to do better).

Using this value, trials were then classified for each participant as representing a Positive Discrepancy (being rated better than you rated yourself), Negative Discrepancy (being rated worse than you rated yourself) or No Discrepancy (no difference between self-rating and judge rating). This classification was based on whether the trial had been a win, lose or neutral ranking, and whether the participants expectancy value indicated that they expected to do better or worse than the others on the attribute being judged in that trial.

Analysis of Behavioural Data

Given the previous findings linking discrepancy and affective disorders, analyses were performed to investigate whether there was a relationship between ratings of emotion on receiving feedback from the judges and the presence (or absence) and direction of any discrepancy. After each trial participants rated their emotional response to the social feedback received. Trials were categorised into those where the participant won or lost, and paired samples t-tests were conducted comparing emotion ratings for discrepant and non-discrepant trials within these categories. Pearson's correlations were run between the discrepancy size and the emotional response scores, again within win or lose categories.

Analysis of Imaging Data

Image preprocessing methods are the same as those utilised in the current protocol, reported in Chapter 3. These are also reported previously in Dalgleish et al. (2017). We corrected for multiple comparisons using a cluster-wise Family-wise error (FWE) threshold of 0.05, using an initial cluster-defining height threshold of $p<0.001$ uncorrected with a *k* cluster extent threshold of 195 voxels (https://zenodo.org/record/1689891#.YUrhE33TU2w).

One Sample T-tests

SPM8 software was used for image analysis. One sample t-tests were carried out to establish differences in activated voxels during Negative Discrepancy, No Discrepancy and Positive Discrepancy trials (Doing worse than expected, as expected, or better than expected, respectively). Batch files were created for each participant individually, within which trials were organised into 3 conditions (named as above). The following feedback contrasts were generated; 'Positive Discrepancy', 'Negative Discrepancy', 'No Discrepancy', 'Positive Discrepancy over Negative Discrepancy'(Pos>Neg), 'Negative Discrepancy over Positive Discrepancy'(Neg>Pos), 'Positive Discrepancy over No Discrepancy' (Pos>No) and 'Negative Discrepancy over No Discrepancy' (Neg>No). For group statistics a voxel-wise statistical threshold of $p<0.05$ familywise error (FWE) was used. Nine Participants did not have any Negative discrepancies and therefore were not included in these contrasts, bringing the participant number down to 47.

Parametric Analysis

To ensure that effects observed in the one-sample t-tests were not the result of feedback-type, a follow up analysis was run which introduced two parametric modulators; feedback type and size of discrepancy.

Batch files were created for each participant individually, and initially each participant's trials were separated into the three trial types as before, this time with the two parametric modulators. However, in several participants the number of trials in each condition was not sufficient, or did not contain a sufficient range of values, to allow a parametric modulation. Therefore, the conditions were combined into a single condition, with trial type as a dummy-coded parametric modulator. The purpose of this modulator was to ensure that the initial findings were not confounded by the absolute rank judgement of each trial (winning/neutral position/losing).

Discrepancy size was also introduced as a modulator; Dalgleish et al. (2017) found in a conjunction analysis of Positive Feedback>Neutral Feedback and Negative Feedback>Neutral Feedback that common areas of activation were present in the dACC and AI. We therefore wanted to examine the effect of discrepancy size irrespective of emotional valence. This was achieved using a quadratic polynomial expansion which considered large positive and large negative discrepancies equally. 10 participants did not have a sufficient range of values to run a quadratic polynomial expansion and could not be included in this analysis, bringing the participant number to 37 for these comparisons. Additionally, we investigated the effect of discrepancy size linearly (aka, which regions are associated with increasing positive discrepancy).

One sample t-tests were computed using the parametrically modulated outputs for the Pos>No and Neg>No conditions. This was so that results could be compared with the non-parametrically modulated results of the initial t-tests, to determine whether trial type had influenced those results. As these tests could only be run with the 37 participants included in the parametric analysis, a second one-sample t-test (as described in section 2.4.1) was run using only these 37 participants for comparison.

Analysis of Variance (ANOVA)

To reduce the number of comparisons in the analysis a one-way, repeated-measures ANOVA was run between Positive, Negative and No Discrepancy trials. The same contrasts as in the initial one-way t-tests were used, and follow up conjunction analyses were run between contrasts. The ANOVA was only conducted on participants with both positive and negative discrepancies, bringing the participant number to 47. A second one-way repeated measures ANOVA was carried out in the same way using only the trials in which participants had received neutral feedback (to remove the effect of feedback type). This analysis was only

conducted on participants who had both positive and negative discrepancies during neutral feedback trials, bringing the participant number to 44.

ROIs

Analysis was carried out using MarsBar in SPM8. ROIs were the dACC and AI regions, as identified by Dalgleish et al. (2017) as the key social "pain and gain" centres (dACC peak voxel x=2, y=32, z=24, left AI peak voxel x=-28, y=18, z=-10). Analyses were performed for the conditions of Positive, Negative, No-Discrepancy, Pos>No and Neg>No.

Regions of the mentalising network were also included as ROIs. A search for "Mentalizing" on Neurosynth (www.neurosynth.org) on the 8th of January, 2018, produced 124 studies. Peak voxel co-ordinates for the dmPFC, vmPFC, Left TPJ and Precuneus were all taken from this map and used to produce 10mm spheres which formed the ROIs (dmPFC x=4/y=52/z=24; vmPFC x=-2/y=48/z=-18; Left TPJ x=-48/y=-56/z=22; Precuneus x=2/y=-54/z=40). Analyses were performed for conditions of Pos>No and Neg>No.

Imaging Analysis: Investigating Behavioural Covariates

As noted, regressions were carried out against two behavioural measures, the Cognitive Emotion Regulation Questionnaire (CERQ) and the Behavioural Inhibition and Approach Scales (Reward-Sensitivity subscale), referred to as the BIS/BAS scales. These measures were selected as regressors on the basis of their relevance to affective disorders and responsiveness to feedback. The nine subscales of the CERQ were separated into those representing adaptive and maladaptive emotion-regulation strategies (Adaptive: Putting into Perspective, Positive Refocusing, Positive Reappraisal, Acceptance, Refocus on Planning. Maladaptive: Self-Blame, Other-Blame, Rumination, Catastrophizing) and scores for each type were averaged for each participant; each participant then had two CERQ scores, one for Adaptive emotion regulation (A-CERQ) and one for Maladaptive (M-CERQ). This method has been validated previously

(Vanderhasselt et al., 2014) and was more appropriate for the current research question than considering subscales individually, in addition to reducing the number of comparisons in the analysis.

Batch files were created in SPM 12 for each discrepancy type (Positive, Negative and No Discrepancy) and for two contrasts (Pos>No, Neg>No). All four regressions were run within each of these five batches. This design allowed us to interpret which of the four regressors had the strongest relationship with the discrepancy types.

2.3. RESULTS

Behavioural Analysis

Analysis of the behavioural data collected by Dalgleish et al. seemed to support the idea that discrepancy affected the participant's emotional experience. After each feedback trial participants rated their emotional response; a paired samples t-test found no significant difference in emotion ratings for win trials with discrepancy compared to those with no discrepancy ($t(259)=1.37$, $p=.17$), however for loss trials, ratings of emotion were significantly lower (i.e. participants felt worse) when the loss represented a discrepancy compared to trials with no discrepancy ($t(259)= 6.07$, $p<.001$, $d=.38$). In addition, a significant correlation was found between the size of the discrepancy and the strength of emotional response, in trials where participants lost this was particularly pronounced ($r=.34$, $n=260$, $p<.001$) but was also true for win trials ($r=-.14$, $n=350$, $p=.007$). So, the larger the discrepancy between your self-ranking and your subsequent social-ranking, the better or worse you felt.

Imaging Analysis

ANOVA

The ANOVA analysis of whole-brain data found that structures of the left dorsal striatum were strongly associated with the Pos>Neg and No>Neg contrasts. The Left Putamen (peak voxel

x=-14, y=8, z=-6) (Figure 2.1A) was significantly activated ($p<0.05$, FWE corrected) for the Pos>Neg contrast (Z=4.86, k=43) and also the No>Neg contrast (-14/10/-8, Z=4.80, k=48). Similarly, the Left Caudate was activated in both the Pos>Neg and No>Neg contrasts (-20/26/-2. Z=4.78, k=11; -14/30/-2, Z=4.81, k=10, respectively). The results of the initial t-tests were used in interpreting the results of the main ANOVA; it is worth noting that in the initial t-tests, the right caudate was also significantly activated for the No>Neg contrast (peak voxel x=26, y=-4, z=24). These results are perhaps unsurprising given the association of these regions with reward processing (Silverman, Jedd, & Luciana, 2015); however, it is interesting that there was no support for a difference in activation between the Positive and No Discrepancy trials. Rather, there was a large decrease in activation for Negative trials (see Figure 2.2 for plot of contrast estimates and 90% confidence intervals of the effects of Interest). In addition to thesestriatal regions, the Pos>Neg contrast also found activation in the Left Medial Frontal Cortex (MFC) (Figure 2.1B), Left Thalamus and Right Precentral Gyrus ($p<0.05$, FWE corrected) (Table 2.1).

A Conjunction analysis was run for activation during the Pos>Neg and No>Neg contrasts. The Left Putamen was again found to be significantly activated in this conjunction (whole brain, $p<0.05$, FWE corrected). At the uncorrected level, the conjunction analysis also found activation in the inferior temporal gyrus (-50/-48/-14, Z=3.76, p=0.05 unc., k=33) and dmPFC (12/28/50, Z=3.53, p=0.05 unc., k=30). These activations were not replicated when considering the Neg>Pos or Neg>No contrasts, and therefore appear to be unique to positive discrepancies.

(A) Left Dorsal Striatum (B) Left Medial Frontal Cortex

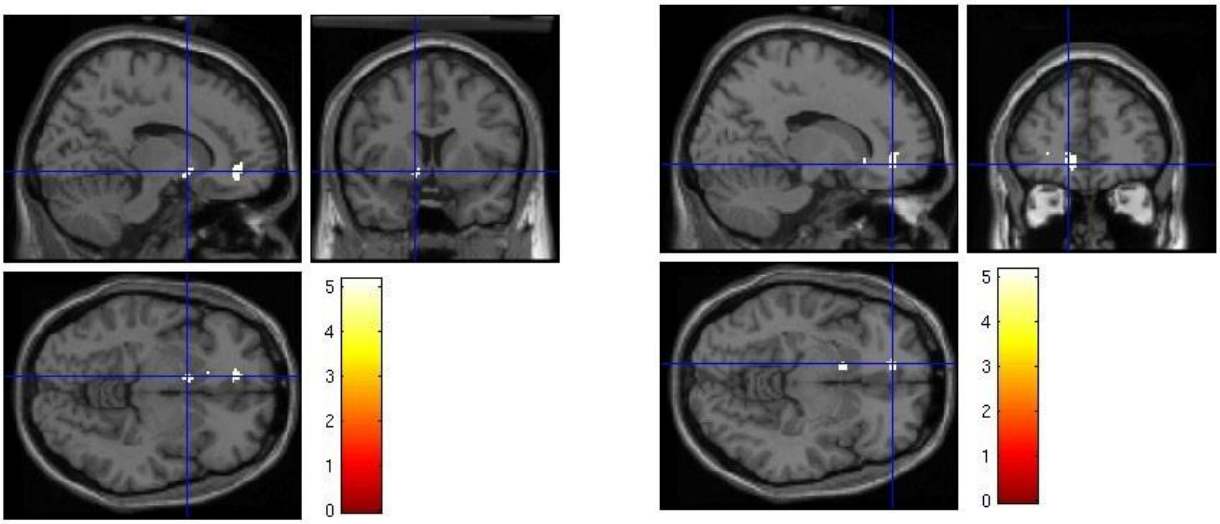


Figure 2.1. ANOVA: Positive> Negative Contrast. (A) Left dorsal Striatum (putamen and caudate). (B) Left Medial Frontal Cortex.

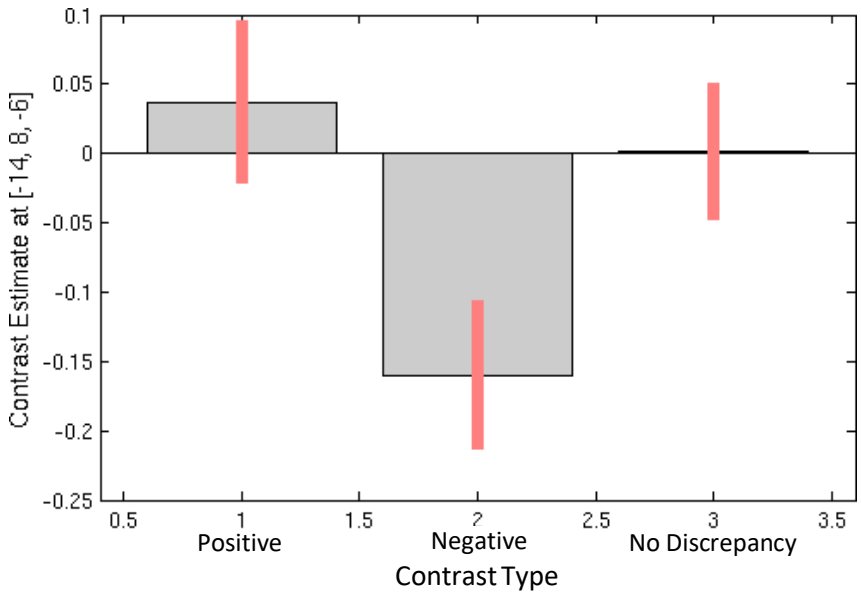


Figure 2.2. Contrast Estimate Plot. Activation of the Left Putamen (x=-14, y=8, z=-6) across the Effects of Interest, showing a drop during negative discrepancy conditions.

The follow up ANOVA, using only the neutral feedback trials, found similar results to those of the initial ANOVA; The Neg>Pos contrast did not find any significant activations, while the Pos>Neg contrast found activation in grossly the same regions, most strongly in the Right Precentral Gyrus (36/-20/46, k=112, p=0.001 unc., Z=3.63) and left Putamen (-14/8/-8, k=40, p=0.001 unc., Z=3.24).

Region	Cluster Size (k)	Z Value	MNI Co-ordinates		
			X	*Y*	*Z*
Positive > Negative					
Right precentral gyrus	32	4.92	24	-10	60
Left medial frontal cortex	59	4.91	-16	44	-8
Left Putamen	43	4.86	-14	8	-6
Left Caudate	11	4.78	-20	26	-2
Left Thalamus	19	4.76	0	-18	8
None > Negative					
Left Caudate	10	4.81	-14	30	-2
Left Putamen	48	4.80	-14	10	-8
Conjunction					
Left Putamen	22	4.78	-14	8	-8
Positive > None					
No Suprathreshold voxels					
Negative > None					
No Suprathreshold voxels					
None > Positive					
No Suprathreshold voxels					
Negative > Positive					
No Suprathreshold voxels					

Table 2.1. ANOVA Contrasts: Whole Brain, p<0.05, FWE corrected level significant

Two regions which initially appeared to be of interest were subsequently discounted. Firstly, in the one-sample tests the left and right supramarginal gyri (SMG) were associated with the Pos>Neg contrast (peak voxels respectively x=-36, y=-28, z=34; x=48, y=-28, z=48). However, the ANOVA found that the SMG was actually deactivated (p<0.05, FWE corrected) across all three conditions, Positive, Negative and No discrepancy (peak voxel x=62, y=-28, z=22). Greater deactivation in the Negative condition explained the findings of the initial t-test but as deactivation was not condition specific the region was not investigated further. Secondly, the right superior parietal lobule (rSPL) was activated in two contrasts in the initial t-tests

(whole brain, $p<0.05$, FWE corrected); for Pos>Neg (peak voxel x=28, y=-50, z=48) and Pos>No (peak voxel x=28, y=-50, z=52). However, activation did not reach FWE significance in the ANOVA for any contrasts and was therefore not investigated further.

A key observation from these results is that the regions identified are distinct from those typically associated with expectancy-violations and those identified by Dalgleish et al's (2017) initial study as signalling social "pain and gain" (most strongly the dorsal anterior cingulate cortex and anterior insula). This provides an encouraging basis for the theory that self-discrepancies are processed separately in the brain.

Parametric Analyses

To ensure that effects observed in the one-sample t-tests were the result of discrepancy, and not simply of receiving positive or negative feedback (feedback-type), a follow up analysis was run which introduced feedback type and discrepancy size as parametric modulators. There were no regions activated to FWE level significance in the parametric analysis, indicating that no additional variance was captured by trial type and degree of discrepancy.

Furthermore, one-sample t-tests of the parametrically modulated outputs for the Pos>No and Neg>No conditions found grossly similar regions of activation to those shown for the same contrasts in the initial t-tests. This was true when the parametrically modulated t-test was compared to the unmodulated t-test of the whole group (N=47), and when compared to just the 37 participants in the modulated sample. This strengthens our inference from the prior analysis, that the initial results were not unduly influenced by trial type.

ROIs

ROI analysis of the Pos>No and Neg>No contrasts found that neither the dACC or AI were significantly activated (Table 2.2) (dACC; Neg>No p=0.999, Pos>No p=0.991; AI; Neg>No p=0.999, Pos>No p=698), and neither were key regions of the mentalizing network, including

the dmPFC (Neg>No p=0.352, Pos>No p=0.995) vmPFC (Neg>No p=0.993, Pos>No p=0.141), Left TPJ (Neg>No p=0.986, Pos>No p=0.436) and Precuneus (Neg>No p=0.917, Pos>No p=0.108). Therefore, none of the six ROI regions was significantly more active in discrepant trials compared to non-discrepant trials. When analysing conditions individually (Pos, Neg and No-discrepancy) all six ROI regions were significantly activated, with the exception of the Left TPJ in the Negative discrepancy condition (t=0.31, p=0.377).

	Contrast Value	T Statistic	Corrected P
Positive > No Discrepancy			
dACC	-0.08	-1.35	0.991
AI	0.00	0.12	0.698
Negative > No Discrepancy			
dACC	-0.19	-3.10	0.999
AI	-0.07	-1.96	0.999
Positive Discrepancies			
dACC	0.20	3.86	0.001
AI	0.25	7.61	0.000
Negative Discrepancies			
dACC	0.09	1.65	0.098
AI	0.17	5.10	0.000
No Discrepancy			
dACC	0.28	5.96	0.000
AI	0.25	8.41	0.000

Table 2.2. Results of the ROI analysis of the dACC and AI

Behavioural Regressors

There were no FWE corrected level activations for the CERQ regression analysis.

In trials which constituted a Negative Discrepancy, a significant relationship was found between lower BIS scores and activation in the right medial frontal cortex, right medial orbital gyrus and right anterior cingulate gyrus (peak voxels x=12, y=40, z=-16, whole brain, p<0.05,

FWE corrected). The BIS measures avoidant behaviours and sensitivity to punishment, therefore low scores might indicate a tendency to be less reactive to negative, punishing or anxiety inducing stimuli (Carver & White, 1994). Possible implications of this are discussed below.

2.4. DISCUSSION

This chapter reports a secondary data analysis of behavioural and fMRI data from Dalgleish et al. (2017) to 1) investigate whether discrepancies between self-perception and social feedback are processed distinctly from absolute feedback type, and 2) identify trait factors which might interact with this processing. We found that several regions of the dorsal striatum and medial frontal cortex (mFC) were significantly less activated in negative discrepancy trials than in positive or no discrepancy trials. Regions typically associated with social "pain and gain" processing did not appear when analysing in terms of discrepancy; the dACC and AI regions were not significantly activated in the parametric or ANOVA analyses. Moreover, an ROI analysis of these regions found that they were not significantly activated for discrepancy over non-discrepancy trials. Both of these results provide no support for the dACC and AI, which are associated with tracking social feedback, being involved in processing the discrepancy such feedback might represent, supporting the idea that a discrepancy of this type might be processed distinctly. One-sample t-tests of the Pos>No and Neg>No contrasts run using the parametrically modulated files produced grossly similar regions of activation as those shown in the non-modulated initial t-test. We can infer then that trial type was not a significant factor in driving our initial results.

Regions of the Dorsal Striatum

The left dorsal striatum and right caudate were associated with various contrasts. The right caudate was associated with the No>Neg contrast. This was the only region specifically

associated with a lack of discrepancy. Berns et al. (2005) investigated activation associated with social conformity scenarios and found that making decisions independent of the group was associated with greater right caudate activity. They interpreted this as being because the experience of social isolation is of high salience. However, alongside the results of this reanalysis, it could be interpreted as representing increased salience of one's own views.

The left caudate was significantly activated during both the No>Neg and Pos>Neg contrasts. Various research seems to support a role of the left caudate in social and emotional processing; Kemp et al. (2013) describe a patient with a focal left caudate lesion who, despite normal performance on neuropsychological tasks, displayed acute social-cognition deficits specific to the "warm" or "affective" aspects of theory of mind. There is also evidence indicating that this region is sensitive to affiliative social relationships; a study by Coan, Schaefer and Davidson (2006) which examined neural activation in response to threat in either the presence or absence of a spouse found that left caudate activation was significantly lower in response to threat when a spouse was present. Moreover, both left and right caudate nuclei have been found to have reduced volumes in patients diagnosed with depression (Krishnan et al., 1992).

The left putamen was associated with the Pos>Neg contrast in the initial ANOVA, again in a follow-up ANOVA using only neutral trials, and at the subthreshold level was associated with increasing size of positive discrepancy in the parametric analyses. These results are perhaps unsurprising given the region's strong generalised association with reward. For example, a study by Izuma, Saito and Sadato (2008) comparing neural responses to social vs. monetary rewards found that the greatest activation and overlap between the conditions was in the left putamen. However, this doesn't rule out a relationship specifically with discrepancy processing. Zucker et al. (2011) monitored neural activity during social interaction with an avatar; the study design comprised four possible scenarios in which the avatar either looked happy or disgusted, while either accepting or rejecting a gift from the participant. They found

that the left putamen was activated for the condition in which the avatar looked happy but subsequently rejected the gift, and that the level of activation in this scenario was greater than for all other conditions combined. This trial was named the "Social Rebuff" and would seem to present a discrepancy between the initial social signal and subsequent behaviour towards the participant. In a study involving self-discrepancies, Shi et al., (2016) presented participants with trait words and had them rate how well they judged each trait to describe themselves. They found that larger discrepancies were associated with activation in the dorsal striatum irrespective of trait valence

Medial frontal cortex

Significant activation was found in several regions of the medial frontal cortices. The left mFC was active in the Pos>Neg contrast, while lower BIS scores were significantly associated with activation in the right mFC during Negative Discrepancy trials. Furthermore, the dorsomedial prefrontal cortex (dmPFC) was selectively activated for Positive as opposed to Negative or No Discrepancy trials. The dmPFC was one of the regions identified by Shi et al., (2016) as being activated when reflecting on traits for which the participant felt a large actual-ideal discrepancy. The dmPFC has been associated with down-regulation of emotion (Kober et al., 2010; Buhle et al., 2013) therefore Shi et al. proposed that it was down-regulating negative affect caused by these large actual-ideal discrepancies. However, down-regulation of emotion in response to a Positive Discrepancy (as in our results) seems counterintuitive; an alternative explanation then might be that the region is involved in coding self-relatedness more generally. The dmPFC has been associated with encoding levels of self-relevance (Northoff et al. 2006, Han & Northoff, 2009) and in the case of Shi et al. increased activation might reflect greater effort to link discrepant traits to one's self-concept. Our results then would be in-line with those of Korn et al (2012) who found that mPFC activation correlated with large discrepancies between self-evaluation and social feedback, and importantly, that the degree of activation

predicted participants positive bias in updating their self-concept. Taken together with evidence linking the dmPFC and mentalising (Muscatell et al., 2012), these results suggest that the dmPFC is involved in interpreting social signals for the updating of self-concepts.

Conclusions and Implications

Socio-evolutionary theories of affect posit that mood states form part of a homeostatic social alarm system, which both detects discrepancies and triggers behavioural and perceptual mechanisms to rectify one's situation (Eisenberger & Lieberman, 2004). Chapter 1 discussed how the Social Risk Hypothesis (Allen & Badcock, 2003) conceptualises depressed mood as one such rectifying mechanism. The mechanism for detecting discrepancies is well explored at the theoretical and behavioural level, in terms of Social Investment Potential, and literature which has linked experiences of rejection, social isolation or low subjective social status with depressed mood (Slavich & Irwin, 2014; Euteneuer, 2014; Matthews et al., 2016). However, previous research at the neural level has tended to focus on the experience of rejection or acceptance without considering whether this information represents a discrepancy which might trigger such mechanisms. The current study aimed to address this issue by reanalysing an existing dataset involving social feedback in terms of whether the feedback was discrepant from participants previous self-ratings. This chapter therefore aimed to identify whether there are specific neural regions for the processing of discrepancies between our self-perception and social-rank feedback.

The results of the analysis found that positive discrepancies were associated with increased activation in regions associated with reward and processing of self-relevance, such as the left putamen, dMPFC and left medial frontal cortex, while negative discrepancies were associated with a fall in activation in regions of the dorsal striatum. Significantly, we found that these regions of activation remained even when controlling for feedback type; we performed

comprehensive analysis controlling for feedback type, using both a parametric modulation of the initial results, and a second analysis in which we only analysed neutral feedback trials. In both cases the regions of activation were grossly similar to those of the initial ANOVA, providing strong support that it was discrepancy, not feedback type, driving this activation.

These findings were unexpected in the context of previous research suggesting a key role for the dACC and AI in processing of social punishment and reward, and in prediction-error, making them a promising candidate for the proposed neural sociometer (Eisenberger, Lieberman & Williams, 2003; Bush, Luu & Posner, 2000).

This analysis therefore produced several goals for the main protocol of the thesis. Firstly, the current dataset only included ratings between one and four, making distinguishing between valence and discrepancy challenging. Secondly, the need for a comparison group of participants with a current depressive diagnosis, to place this discrepancy mechanism within the context of socio-evolutionary theories. Finally, the need to distinguish between intrapersonal and interpersonal discrepancies, and their varying roles in forming and maintaining a self-concept set-point. The following Chapter, Chapter 3, will describe how the main protocol of the current thesis addresses each of these issues through the collection of new data.

CHAPTER 3. GENERAL METHODOLOGY AND EVIDENCE OF AFFECTIVE AND SOCIAL PROCESSING BIASES

3. 1. INTRODUCTION

This chapter outlines general procedures pertaining to the main protocol presented in this thesis. This protocol integrated several tasks across two days, collecting neuroimaging, self- report, and behavioural data, with the same participants and procedures for recruitment and ethical considerations. This overview will place these tasks within the broader context of the protocol. Additionally, this chapter will discuss the findings of 6 affective and social processingmeasures administered across all participants, and consider their implications for our understanding of social affective processing biases in depression, and validation of these measures in a clinical sample.

Chapter 1 discussed The Social Risk Hypothesis of Depressed Mood (SRH; Allen & Badcock, 2003), which conceptualises depressed mood as an adaptive response to critically low social rank, that protects against the risk of exclusion by promoting rank-appropriate behavioural strategies. This includes engaging in submissive affiliative behaviours, which is supported by studies finding preferential attention to affiliative cues under the threat of exclusion (DeWall et al., 2009). In support of the SRH, perceptions of low social rank have been associated with depression (Wood & Irons, 2015) and severity of depressive symptoms has been found to correlate with sensitivity to social rejection (Luty, Joyce, Mulder, Sullivan & Mackenzie, 2002), moreover, interpersonal difficulties are a key psychosocial risk factor for the development of depression (van Harmelen et al., 2016). Further discussion of this evidence can be found in Chapter 1.

The studies reported in this thesis used a number of measures to assess perceived social status, in addition to clinical measures of affective symptoms. These included the Submissive Behaviour Scale (SBS; Allan & Gilbert, 1997), Striving to Avoid Inferiority Scale (SAIS; Gilbert, Broomhead, Irons & McEwan, 2007), Interpersonal Sensitivity Measure (IPSM;

Boyce & Parker, 1989) and Involuntary Subordination Questionnaire (ISQ; Sturman, 2011). These inventories assess distinct but inter-related aspects of social behaviour relevant to the central research questions under analysis here. Previous findings have supported the relationship between these measures and depressive symptoms; however, research administering these measures within depressed samples is currently limited. The ISQ correlates with self-criticism and low self-esteem (Sturman, 2011). Insecure striving to avoid inferiority has been positively associated with depressive symptoms and fear of rejection (Gilbert et al., 2007) while secure non-striving shows negative associations with these same characteristics (Bellew, Gilbert, Mills, McEwan & Gale, 2006). Interpersonal sensitivity is shown to be heightened in Depression (Luty et al., 2002); however, many of these studies focus on the concept's relationship with social anxiety (Vidyanidhi & Sudhir, 2009). Use of these measures is crucial in characterising the impairments in social functioning present in Depression.

To characterise the clinical features of the participant samples, the work reported here additionally utilises the Beck Depression Inventory-II (BDI-II; Beck, Steer & Brown, 1996) and Beck Anxiety Inventory (BAI; Beck, Epstein, Brown & Steer, 1988) to assess symptom severity and presence of symptoms across group..

Perfectionism was assessed due to it's relevance to the theme of discrepancy considered in this thesis (Hewitt, Flett & Mikhail, 2017) and its robust associations with social rank variables and mood disorders (Smith et al., 2018; Wyatt & Gilbert, 1998). The Hewitt-Flett Perfectionism Scale (Hewitt & Flett, 1990) was utilised, as this measure assesses three dissociable forms of perfectionism: Self-Orientated Perfectionism (SOP; demanding perfection from oneself), Other-Orientated Perfectionism (OOP; demanding perfection from others) and Socially Prescribed Perfectionism (SPP; believing others have high standards for you, and judge you stringently upon these). Of these, SPP is the strongest predictor of Depression (Smith et al., 2016) and is associated with social rank variables including negative evaluations of social

comparisons, submissiveness, shame, and defeat (Wyatt & Gilbert, 1998). Explanations for the relationship between SPP and Depression have focused on the role of interpersonal discrepancies, that is, beliefs that you will fall short of other's expectations, which precipitates negative expectations about one's ability to succeed in social contexts (Smith et al., 2018). These are characterised in the Perfectionism Social Disconnection Model as two key triggers for Depression: interpersonal discrepancies and social hopelessness (Hewitt, Flett & Mikail, 2017). A cognitive predisposition to make unfavourable social comparisons and feelings of being negatively evaluated by others are relevant within the current thesis in relation to perceptions of social rank and status, and the particular importance of discrepancy in homeostatic theories of mood.

Overall, this chapter has two aims. First to characterise the overall sample and methods used to form the studies reported in the rest of the thesis. Second, to present data on broad self-report measures of affect, social functioning and perfectionism, alongside clinical measures, to replicate previous work suggesting that Depression is associated with systemic biases in social affective processing and cognition, and validate previous findings relating to inferiority, involuntary subordination, submissive behaviour, and interpersonal sensitivity. Based on the hypotheses of the SRH we predicted that our Depressed group would score more highly on each of these measures than the Control group.

3. 2. PROTOCOL OVERVIEW

The protocol for the studies reported here ran over two days and consisted of five tasks (Figure 3.1). The first day was a group behavioural testing session, in which five participants from the same experimental group (Control or Depressed) performed two social neuroeconomic games and completed questionnaires relevant to the following day's tasks. The second day was an

fMRI scanning session which participants attended individually, involving three tasks. Therefore, five individual scanning sessions were run consecutively on the second day. Both the first and second day sessions lasted 90 minutes.

Pre-Session Social and Affective Questionnaires: Beck Depression Inventory – II (BDI-II; Beck, Steer & Brown, 1996), Beck Anxiety Inventory (BAI; Beck, Epstein, Brown & Steer, 1988), Submissive Behaviour Scale (SBS; Allan & Gilbert, 1997), Involuntary Subordination Questionnaire (ISQ; Sturman, 2011), Interpersonal Sensitivity Measure (IPSM; Boyce & Parker, 1989), Striving to Avoid Inferiority Scale (SAIS-I; Gilbert, Broomhead, Irons & McEwan, 2007)			
Day 1 – Group Behavioural Testing Session (70m tasks + 20m additional)			
10m	25m	15m	20m
(1) Self-Rating Sheet	(2) Public Goods Game	(3) Balloon Analogue Risk Task	(4) - Self-Other Ratings Sheet - Demographic Questionnaire (Narcissism and Perfectionism Scales) (5) - Ultimatum Game: Offers Sheet

Day 2 – Individual fMRI Scanning Session (70m tasks + 20m additional)				
10m	20m	30m	5m	5m
(1) Actual-Ideal Selves Task	(4) Social Feedback Task	(5) Ultimatum Game: Responder Task	Structural Scans (not reported)	Post-Scan Believability Questionnaires

Figure 3.1. Protocol Overview. Tasks 1, 4 & 5 involved behavioural and scanning components. Both sessions lasted 90 minutes, allowing 70 minutes of tasks and 20 minutes for changing between tasks, obtaining consent and debriefing.

Design Rationale

The design of this protocol is unusual amongst the existing literature on social and affective processing. Much of this literature has investigated social behaviours by observing interactions with unknown computerised agents; participants are often told that their partner is a fellow

participant, a stranger they have not seen, met, or spoken to prior to the task. This methodology is common across the Ultimatum Game, Public Goods Game and Social Inclusion and Rejection literature (Robson et al., 2020). The advantage of these designs is that a participant's prior knowledge of their partner is controlled for, and set-up and execution of the task is efficient. However, there are serious concerns regarding the ecological validity of a design which uses strangers or fictitious participants as a context for examining social and affiliative behaviours (Hermans et al., 2019). Moreover, evidence from modelling of these tasks has implied that the development and observation of reciprocal social relationships may be hampered when one player's responses are computer automated (Silverman, 2018).

The current protocol attempted to address these concerns by creating a novel social context for testing; the behavioural session on the first day was completed with groups of five participants, which allowed them to communicate and form social associations, with the Public Goods Game creating opportunities for further interaction amongst the group. Mental health status was consistent within groups, so that cooperative behaviours in Depressed and Control groups could be observed independently. In addition, this design allowed us to collect a unique cross-task dataset, comprising behavioural data from multiple neuroeconomic games alongside neuroimaging data. Such a design presents significant logistical challenges, which are further complicated by the inclusion of clinical participants and the associated difficulties in recruitment and ethical provisions.

Social Tasks

Actual-Ideal Selves Task (Chapter 4)

Self-concept discrepancy theory (Higgins, 1987) proposes that we have different instantiations of self-concept, including an Actual Self, representing how we believe ourselves to be in reality, an Ideal Self, representing our goal self, and an Ought Self, of how we believe we

should be. According to Higgins' theory, discrepancies between these self-models confer distinct negative psychological and emotional states. Discrepancies between Ideal and Actual self-concepts have been associated with depressive symptoms (Watson, Bryan & Thrash, 2016). The purpose of this task was to extend the limited existing neuroimaging research on this discrepancy, within the context of the homeostatic theories of self-concept and social status addressed in Chapter 1.

The protocol for the task was modelled on Shi et al. (2016). During the behavioural session, participants rated their Actual Self on 24 positive and 24 negative trait adjectives (see below for details on trait adjective selection and rating), on a 1-10 Likert scale where 1 indicated "Not like me" and 10 indicated "Very much like me". During the scanning session, participants were visually presented with each of these trait words. Using a button box, they indicated how far they felt their Actual Self was from their Ideal Self on that trait, on a scale from 1 to 4, where 1 indicated very close and 4 indicated very far.

The task is described in more detail in Chapter 4.

Public Goods Game (Chapter 7)

Public Goods Games are a form of neuroeconomic game which examine the tendency to cooperate in the presence of an incentive to defect. Participants contribute resources to a group pot, which is then multiplied and shared equally; at the individual level, zero contributions will produce the best outcome for a player. However, at the group level, the highest gains are achieved when everyone contributes the maximum every time. The purpose of this task was twofold, firstly, to examine cooperative behaviour in depressed participants, as a possible method of social risk avoidance in accordance with the predictions of the SRH. Secondly, to investigate the outcome of this task within clinically homogenous groups, in contrast to previous designs where all but one player is computer automated.

Participants completed the task on individual laptops, seated in an open plan testing room with their fellow group members. The task was a standard linear Public Goods Game of 10 rounds, and participants were endowed with 20 tokens at the start of the task with a monetary value of £0.05 each. Each round consisted of four screens; Screen One displayed the current totals of each group member and asked participants to decide their contribution amount. Screen Two displayed the overall total in the pot, the multiplied value of the pot, each member's share (an equal split) and the updated totals of each member. Screen Three asked participants if they wished to use a token to punish another group member; doing so would deduct 2 tokens from that group member. Screen Four displayed final totals, which carried over into the next round.

The task is described in more detail in Chapter 7.

Balloon Analogue Risk Task (Chapter 8)

The Balloon Analogue Risk Task (BART) (Lejuez et al., 2002) is a behavioural measure of risk-taking under experimental conditions. The task has been shown to correlate with trait measures of risk taking and real-world risk-taking behaviours such as drug abuse (Hopko et al., 2006; Aklin et al., 2005) and has better test-retest reliability than other measures of risk- taking (Xu et al., 2013). The purpose of this task was to investigate the hypotheses of the SRH regarding reduced social risk-taking in depression by applying a novel social adaption of the task within a depressed sample. Participants played the game on individual testing laptops in a shared open-plan testing room. The game involved pumping up a computerised balloon through repeated keypresses to earn tokens; larger balloons earned more tokens but were more likely to pop. Participants played two iterations of the game, one Individual version, where tokens gained were kept for themselves, and one Social version where wins would be shared and publicised to the group.

The task is described in more detail in Chapter 8.

Social Feedback Task (Chapter 5)

The Social Feedback Task is a novel protocol which involved presenting individuals with feedback on socially relevant trait characteristics ((see below for details on trait adjective selection and rating). The purpose of this task was to investigate differences in neural responses to social feedback in our samples, and to extend research which has aimed to identify a neural signature for a Sociometer or for self-other discrepancies. There were two feedback conditions for this task; a Social condition, in which participants received feedback from their groupmates, and a Demographic condition, in which participants received feedback of how they scored relative to others in their demographic group, based on an objective scientific measure (a questionnaire). For ethical reasons, the depressed sample only completed the Demographic condition while the Control group completed both conditions.

During the behavioural session, all participants completed two measures for use in this task. First was the Self-Other Ratings Sheet; this sheet asked them to rate themselves and their group mates on 20 socially relevant trait adjectives, from 1 to 10, 1 being "Not at All Like Me/Them", and 10 being "Very Much Like Me/Them". The purpose of this sheet was to collect self-ratings, and to create believability for the feedback subsequently presented in the Social condition. Second was a "Demographic Questionnaire", which participants were told was a widely used questionnaire designed to rank individuals relative to the rest of the population on various traits. This questionnaire was in-fact two unrelated measures (The Narcissistic Personality Inventory and Hewitt-Flett Perfectionism Scale) and was administered in this way to create believability for the feedback presented in the Demographic condition. During the scanning session on day 2, participants were presented with feedback for the 20 trait adjectives they had rated themselves on the previous day (10 in the Demographic Condition, 10 in the Social Condition). For each trait, participants viewed 6 slides. First, a Self-Rating Reminder slide, which displayed their self-rating from the previous day. Then, four feedback slides; in the social condition,

feedback slides showed the identity of the rater (a group mate) and their rating of the participant, while in the demographic condition, feedback slides showed the demographic group they were being compared to (Age, Gender, Education Level, Employment) and their rating within that group. The final slide gave participants the option to re-rate themselves using the same scale as before, via a button box.

The task is described in more detail in Chapter 5.

Ultimatum Game (Chapter 6)

The Ultimatum Game is a well-established neuroeconomic game involving two players, in which the Proposer suggests a division of money between themselves and their partner, the Responder. However, each only receives the money if the Responder accepts the division, otherwise neither receives anything. This task reliably produces findings interpreted to support theories of human altruism and reciprocity over economic rationalism (Camerer & Fehr, 2004). The purpose of this task in the current context was to investigate the prediction of the SRH that individuals with Depression will more effectively improve their social value and avoid exclusion, potentially through upholding social norms and displaying prosocial behaviours. It also allowed us to further examine neural activity during social norm violations in Depression. During the behavioural session, participants completed the Offers Sheet, in which they played a one-shot version of the game as the Proposer against each of their fellow participants and anonymous strangers. During the scanning session, participants were presented with the offers they had received from their fellow participants and anonymous strangers, and played as the Responder, choosing to accept or reject the offers using a button box. The scanning aspect of this task was modelled on Gradin et al. (2015).

The task is described in more detail in Chapter 6.

Trait Word Selection

The Actual-Ideal Selves Task and the Social Feedback Task both involved participants rating themselves on trait characteristics, and then reflecting or receiving feedback on those traits. It was important that these traits were considered socially valuable, and possible factors in determining one's social rank. To select the traits used in these tasks, a sample of 40participants (22 female, age range 20-62, mean=42) were administered candidate items for thedevelopment of The Social Values Questionnaire (Griffiths et al., in prep) (Appendix 3.1). Thequestionnaire development required participants to rate 142 trait words across 7 domains (Affiliation, Individualism, Agency, Intelligence, Conversation, Anti-Social, Dominance and Social-Media) with respect to their social value on a 7-point Likert scale from 'Not valuable' to 'Highly Valuable'. The 68 words with the highest and lowest value scores were extracted. Within each valence group (Most valuable/Least valuable) 24 words were pseudo-randomly selected for inclusion in the Actual-Ideal task (n=48), and the remaining 10 used in the Social Feedback Task (n=20).

Statistical Analysis

Across the thesis, an alpha level of p=0.05 was set as the statistical significance threshold for behavioural data, unless otherwise specified, and a Bonferroni correction applied to correct for multiple comparisons where appropriate. For neuroimaging data, at the whole-brain level, we used a FWE cluster-wise threshold ($p<0.05$) for all analyses. FWE rate cluster size was determined for each analysis using Zenodo v1.0 (Philips, 2018) and is specified in each chapter results section where appropriate. This approach is strengthened by region of interest analyses across the chapters. Exploratory data analysis ensured that the data met criteria for parametric analysis, utilising Levene's test of homogeneity of variance and Kolmogorov-Smirnov's test of normality. Mauchlys test of Sphericity was used to assess assumptions of sphericity, where this was violated and the correction used are reported in the text. Demographic data were analysed using a Pearson's Chi-square test to assess differences in gender, ethnicity or

education level between groups, and independent samples t-tests were used to assess differences in age and our key measure of clinical symptoms, the BDI-II. One-way analyses of variance (ANOVA) and mixed between- and within-subject ANOVAs were used to investigate group differences across tasks, as outlined in the relevant chapters.

A-priori power analyses are complicated by the difficulties of controlling sample sizes when testing vulnerable groups (Philips, 2012). Post-hoc power analyses were conducted using the given sample sizes, the 0.05 statistical significant threshold and a medium effect size (0.25), and implemented using the software package GPower (Faul, Erdgelder, Buchner & Lang, 2009). The achieved power across studies are shown in Table 3.1.

Study	Chapter	*N*	Controls	Depressed	Power
Questionnaire Measures	3	*62*	32	30	96%
Actual Ideal	4	*50*	25	25	82%
Social Feedback	5	*62*	32	30	87%
Ultimatum Game	6	*58*	33	25	90%
Public Goods Game	7	*50*	25	25	79%
Balloon Analogue Risk Task	8	*62*	32	30	91%

Table 3.1. Sample Sizes and Post-Hoc Power Analyses for key analyses across all studies

Image Preprocessing

MRI scanning was conducted at the Medical Research Council Cognition and Brain Sciences Unit on a 3-Tesla Tim Trio Magnetic Resonance Imaging scanner (Siemens, Germany) by using a head coil gradient set. Whole-brain data were acquired with echoplanar T2*-weighted imaging (EPI), sensitive to BOLD signal contrast (48 sagittal slices, 3mm thickness; TR= 2000 ms; TE= 30 ms; flip angle= 78°; FOV 192 mm; voxel size: 3× 3× 3 mm). To provide for equilibration effects the first 5 volumes were discarded. T1 weighted structural images were acquired at a resolution of 1×1×1mm. SPM8 software (www.fil.ion.ucl.ac.uk/spm/) was used

for data analysis. The EPI images were sinc interpolated in time for correction of slice timing differences and realignment to the first scan by rigid body transformations to correct for head movements. Field maps were estimated from the phase difference between the images acquired at the short and long TE and unwrapped, employing the FieldMap toolbox. Field map and EPI imaging parameters were used to establish voxel displacements in the EPI image. Application of the inverse displacement to the EPI images served the correction of distortions. Utilising linear and non-linear transformations, and smoothing with a Gaussian kernel of full-width-half-maximum (FWHM) 8-mm, EPI and structural images were co-registered and normalised to the T1 standard template in Montreal Neurological Institute (MNI) space. Global changes were removed by proportional scaling and high-pass temporal filtering with a cut-off of 128 s was used to remove low-frequency drifts in signal.

3. 3. PARTICIPANT SAMPLE

Demographics

Demographics of the full participant sample are summarised in Table 3.2. This sampleremained the same throughout the protocol, however, small variations occurred in some tasks as a result of difficulties in data acquisition or reporting non-belief of manipulations. These variations are detailed in their respective chapters. In the full sample, participants were 62 adults (38 female, age range 18-74, mean=45.77yrs) recruited from the MRC CBU volunteer panel. This comprised 32 never-depressed Control participants (20 female, age range 18-64, mean=44.85yrs) and 30 Depressed participants (18 female, age range 21-74, mean=47.44yrs). There were no significant differences between the groups in relation to gender ($X^2(1, N=62)=.027$, $p=.87$), age ($t(60)=-.75$, $p=.46$), education level ($X^2(1, N=62)=4.48$, $p=.34$) or ethnicity ($X^2(1, N=62)=7.77$, $p=.10$). For both groups, inclusion criteria were normal or corrected-to-normal vision, being over 18 years and English speaking. Exclusion criteria for

both groups were current experience of psychosis, alcohol or drug use disorder, major neurological condition, diagnosed specific learning disability or failure of MRI safety screening.

Variable	Controls (n=32)	Depressed (n=30)	Between Groups Tests	Total (n=62)
Age				
Mean	44.85	47.44	t(60)=.75	45.77
Range	18-64	21-74		18-74
Gender *n* (%)				
Female	20 (63.6)	18 (61.5)	X^2= .027	38 (62.7)
Male	12 (36.4)	12 (38.5)		24 (37.3)
Ethnicity				
% Caucasian	27 (84.4)	26 (86.6)	X^2=7.769	53 (85.5)
% Chinese	3 (9.4)	-		3 (4.8)
% South Asian	2 (6.2)	-		2 (3.2)
% Mixed	-	4 (13.3)		4 (6.5)
Education				
% GCSE	9 (28.2)	7 (23.3)	X^2=4.483	16 (25.8)
% A Level	10 (31.2)	6 (20.0)		16 (25.8)
% Bachelors	6 (18.8)	4 (13.4)		10 (16.2)
% Masters	5 (15.6)	6 (20.0)		11 (17.7)
% PhD	2 (6.2)	7 (23.3)		9 (14.5)
BDI-II				
Mean (SD)	5.45 (4.52)	27.61 (10.96)	t(31.7)= 9.674**	
Range	0-16	13-53		

Table 3.2. Participant Demographics. BDI-II: Beck Depression Inventory (Beck, Steer & Brown, 1996) Minimal Range: 0-13, Mild Range: 14-19, Moderate:20-28, Severe: 29-63. ** indicates p<0.01

Recruitment

Recruitment took place in Cambridge, UK. Healthy Controls were recruited from the department participant panel at the MRC Cognition and Brain Sciences Unit (CBU) at the University of Cambridge. Volunteers for the department participant panel were recruited via the MRC CBU website, local advertisements, open-days and word-of-mouth. Depressed

participants were recruited from the Cognition, Emotion and Mental Health research group depression panel. This panel includes participants who have previously met criteria for a diagnosis of Major Depressive Disorder (MDD), as determined by the Structured Clinical Interview for the DSM-5 (SCID; First, Williams, Karg & Spitzer, 2015). The SCID is a standardised diagnostic interview involving a series of questions concerning a range of past and present symptoms. The interview is administered after comprehensive training and can assist in making reliable DSM-5 psychiatric diagnoses. Participants with diagnoses of psychosis, bipolar disorder, personality disorder or drug or alcohol problems are not eligible for the depression panel.

Inclusion criteria for the Depressed group was a diagnosis of MDD with a current episode, as determined by the Structured Clinical Interview for the DSM-5 (SCID; First, Williams, Karg & Spitzer, 2015). Presence of a current major depressive episode was confirmed shortly prior to testing through re-administration of the mood module of the SCID. The Depressed group had an average BDI-II score of 27.61, falling on the higher boundary of the moderate range (20-28), which was significantly different to the Control group average of 5.45 ($t(31.7)= 9.67$, $p=<.001$). Exclusion criteria for the Control group was any current Axis 1 psychiatric disorder according to the Diagnostic and Statistical Manual of Mental Disorders (DSM-5). The distribution of BDI-II scores is shown in Figure 3.2 and detailed in Table 3.3.

Severity	**Control**	**Depressed**	**Total**
Minimal (0-13)	30	3	33
Mild (14-19)	2	5	7
Moderate (20-28)	-	9	9
Severe (29-63)	-	13	13
Total	*32*	*30*	62

Table 3.3. Distribution of BDI-II Severity within Groups

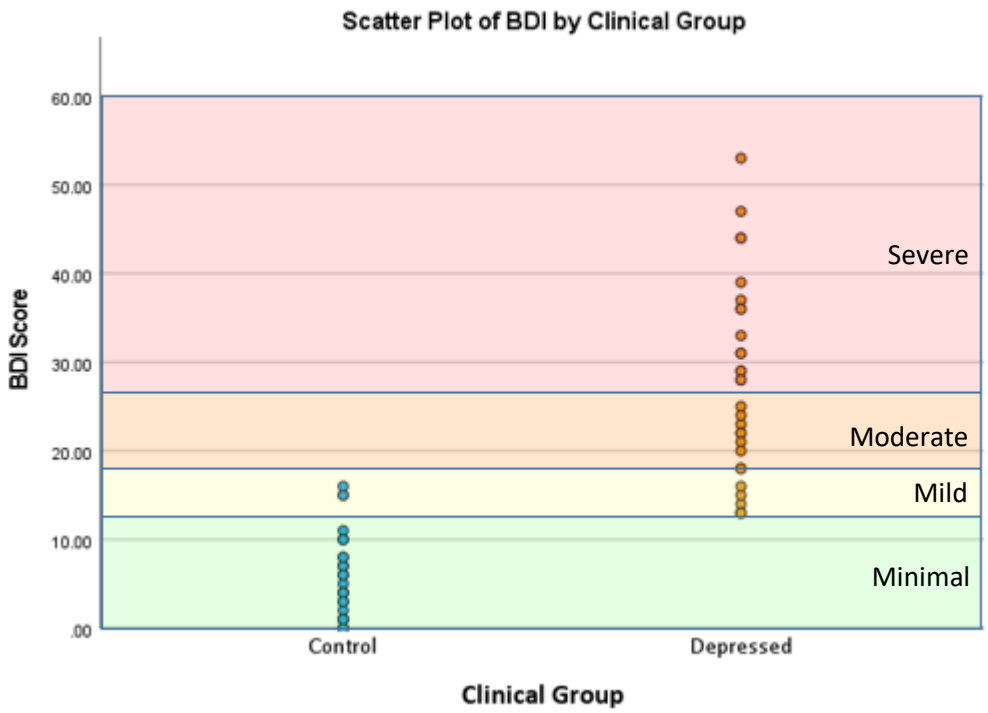


Figure 3.2. Scatter Plot of BDI by Clinical Group. Cut-offs for each level of Severity, Severe, Moderate, Mild and Minimal are shaded in Red, Orange, Yellow and Green respectively

Matching of the Control sample was done at the group level, on the basis of age, gender and educational background. Participants were emailed and invited to a telephone screeningsession. Individuals were administered the Mood Module of the SCID via telephone and eligible participants invited to take part. All participants completed all experiments, with the exception of the Social Condition of the Feedback Task, which was only completed by the Control Group. Participants were paid £32 for completion of *both* behavioural and neuroimaging sessions, constituting £6/hour for behavioural studies (minimum £12 guaranteed) and £10/hour for neuroimaging (minimum £20 guaranteed), in addition to travel expenses. Payment details were taken on the second day after scanning, to discourage drop-outbetween sessions 1 and 2.

Medication and Comorbidities

The Control group indicated no past or current use of antidepressant medication, while 47% of the Depressed group reported current use (Table 3.4). Antidepressants may be associated with emotional blunting (Sansone and Sansone, 2010), and can limit the generalisability of neuroimaging findings (Hughes-Morley, Young, Waheed, Small & Boewr, 2015). However, recruiting a medication naïve sample can also limit the representativeness of the sample, given the widespread use of medication for the treatment of Depression (Luo et al., 2020), and presents additional difficulties in the recruitment of clinical subjects.

	N (Total N=30)	**Min Dosage (mg/day)**	**Max Dosage (mg/day)**
Citalopram	5	20	30
Venlafaxine	3	30	375
Mirtzapine	2	15	30
Fluoxetine	2	10	30
Sertraline	1	100	100
Other	1	-	-
Total	***14***		

Table 3.4. Medication use in the Depressed sample

Co-morbidity amongst affective disorders is common; as many as 80% of individuals with Depression are diagnosed with an anxiety or other related disorder (Gaderman et al., 2012). Therefore, participants with common co-morbidities were not excluded, in line with existing social affective literature (Table 3.5).

Comorbidity	Past	Current	Total
Eating Disorder	2	2	4
Generalized Anxiety Disorder	2	3	5
Obsessive-Compulsive Disorder	0	1	1
Panic Disorder	1	1	2
Post-Traumatic Stress Disorder	1	2	3
Social Anxiety Disorder	1	0	1
Total	*7*	*9*	17

Table 3.5. Co-Morbidities in the Depressed sample

Ethical Considerations and Confidentiality

One element of the protocol, the Feedback task, involved participants receiving feedback on several trait characteristics. Negative social feedback of this kind can elicit strong negative emotions, so to avoid Depressed participants becoming overly distressed, only the Control group were included in the Social condition of this task. Questionnaires involving self-reflection on negative moods and stress can also lead to negative affect, however, these measures are widely used in personality research with no reported long-term negative outcomes. Testing of clinical groups was carried out under the supervision of on-site clinical psychologists (Dr Tim Dalgleish, Dr Caitlin Hitchcock, Dr Melissa Black; Dr Anna Bevan). Participants reporting suicidal thoughts or wishes on question 9 of the BDI-II, or experiencing significant distress during the tasks, had a confidential consultation with a clinical psychologist before leaving the testing centre. In the event that significant abnormalities in the structural MRI data were identified by the MRI operator, this was brought to the attention of the CBU medical monitor, who was responsible for acting on the information. Full details of mood and imaging protocols for adverse events can be found in Appendices 3.2 and 3.3.

To ensure confidentiality of participants, individuals were assigned ID numbers during the task which were linked with data collected during the study, in order to separate their personal

information. Data were held on secure servers located at the CBU, and any paper-format behavioural data was kept in a locked filing cabinet until it could be scanned or entered manually onto these servers.

Participants were informed that the purpose of the task was to investigate social interactions and mood. All participants provided written informed consent and were fully debriefed on the manipulation of feedback and offers following completion of the tasks, in addition to receiving a debriefing sheet. Consent forms, information sheet and debriefing sheet can be found in Appendices 3.4, 3.5 and 3.6. The study was approved by the Cambridge Psychology Research Ethics Committee (CPREC; PRE:2017.083), and the ethics application can be found in Appendix 3.7.

3.4. SELF-REPORT MEASURES

Mood Measures

Beck Depression Inventory- II (BDI-II: Beck, Steer & Brown, 1996) (Appendix 3.8)

The BDI-II is a 21-item self-report inventory, widely used for assessing severity of depression in adolescent and adult populations. Although the BDI-II is not a diagnostic tool, it has been found to have high validity in discriminating between Depressed and subclinical subjects (Lasa et al., 2000), in addition to high test-retest reliability, ranging between 0.73 to 0.96, and internal consistency around 0.9 (Richter et al., 1998; Storch et al., 2004; Wang & Gorenstein, 2013).

Beck Anxiety Inventory (BAI: Beck, Epstein, Brown & Steer, 1988) (Appendix 3.9)

The BAI is a 21-item self-report inventory for assessing the severity of anxiety symptomology, referring to symptoms experienced during the previous week. The BAI has been shown to have high internal consistency and retest reliability (Osman et al., 2002) and is significantly less

confounded by depressive symptoms than other measures of anxiety (Fydrich, Dowdall & Chambless, 1992).

Social Measures

Submissive Behaviour Scale (SBS: Allan, S. & Gilbert, P., 1997) (Appendix 3.10)

The SBS is a 16-item measure, based on the submissive behaviours identified by Buss and Craik (1986), which assesses submissive social behaviour. Participants rate the frequency with which they exhibit examples of submissive behaviour on a scale of 0 to 4, where 0 indicates "Never" and 4 indicates "Always". Gilbert et al. (1996) found the scale had high retest reliability over a four-month period (r=.84).

Involuntary Subordination Questionnaire (ISQ: Sturman, E., 2011) (Appendix 3.11)

The ISQ is a 32-item inventory which measures feelings of inferiority, entrapment, defeat and submissive self-perceptions. The ISQ has high levels of internal consistency and test-retest reliability, correlates with dominance and neurotic personality styles, and has been found to be predictive of social anxiety (Sturman, 2011). This measure has not been widely used with depressed samples, and its use here aims to examine the relationship between subordination and depressed mood.

Interpersonal Sensitivity Measure (IPSM: Boyce, P. & Parker, G., 1989) (Appendix 3.12)

The IPSM is a 36-item inventory which assesses sensitivity to social feedback and interpersonal behaviour across five sub-scales; interpersonal awareness, separation anxiety, timidity, need for approval and fragile inner-self. High scores on this scale are indicative of higher awareness and sensitivity of others, which in the context of the SRH might represent an adaptive response to social risk. The scale has been shown to have high internal consistency in both depressed (0.86) and control (0.85) samples (Harb et al., 2002).

Striving to Avoid Inferiority Scale (SAIS-I: Gilbert, Broomhead, Irons & McEwan, 2007) (Appendix 3.13)

The SAIS-I is a 31-item self-report inventory which measures two factors relating to inferiority; insecure striving, striving based on fear of rejection or criticism, and secure non-striving, a feeling of being socially acceptable regardless of success or failure. Gilbert et al. found that both factors were significantly related to fears of rejection, need for validation and feelings of inferiority, and significantly predicted psychopathologies. This measure has been validated for use in both depressed (Williams et al., 2009) and healthy populations (Gilbert et al., 2009).

Perfectionism

Hewitt-Flett Multidimensional Perfectionism Scale (MPS: Hewitt, P. & Flett, G., 1990) (Appendix 3.14)

The MPS is a 45-item self-report inventory which measures three dimensions of perfectionism; self-orientated perfectionism, other-orientated perfectionism and socially-prescribed perfectionism. The scale has demonstrated reliability and validity across various contexts (see Hewitt & Flett, 2004, for a review) and the three dimensions of the scale are stable in both clinical and non-clinical subjects (Hewit, Flett, TurnBull-Donovan & Mikhail, 1991).

Data Analysis

Kolmogorovs-Smirnov's test of normality and Levene's test of homogeneity of variance found that questionnaire ratings were normally distributed and homogenous across groups. Pearson Correlations were calculated between all social and affective questionnaires, both across and within groups, to investigate their degree of association. Independent groups t-tests were used to identify differences on questionnaire scores between groups. Correlations were performed

between these measures and the Perfectionism subscales to investigate the relationship between these variables, both across and within groups.

Relationship between Social and Mood Measures

Social Rank Measures

Across the whole sample there was a strong correlation (to $p<.001$ level) between all 6 social measures (Table 3.6). All of the individual correlations were of a large effect size ($d>0.8$) with the strongest effect sizes found between the BDI-II and ISQ (r=.85, p<.001) and IPSM and SBS (r=.75, p<.001).

Measure	*M*	*SD*	BAI	BDI-II	IPSM	ISQ	SAIS:I	SAIS:S
1.BAI	9.02	8.24						
2.BDI-II	15.22	13.65	.65**					
3.IPSM	103.74	14.78	.59**	.70**				
4.ISQ	84.56	21.05	.51**	.84**	.74**			
5.SAIS:Insecure	37.76	15.22	.47**	.55**	.55**	.65**		
6.SAIS:Secure	29.30	10.96	-.39**	-.67**	-.48**	-.62**	-.48**	
7.SBS	27.08	11.01	.58**	.73**	.75**	.75**	.54**	-.58**

Table 3.6. Across-Group Correlations between Social Questionnaires. ** indicates $p< .01$. *M* and *SD* represent the mean and standard deviation respectively.

Independent groups t-tests found a significant difference between the Depressed and Control Groups on all 6 measures (Table 3.7), with Depressed participants scoring higher on all measures except the SAIS:Secure subscale.

	Controls		*Depressed*			
Measure	*M*	*SD*	*M*	*SD*	t statistic	*d*
1.BAI	4.78	6.03	14.60	7.36	5.57**	1.11
2.BDI-II	5.45	4.52	27.61	10.97	9.67**	1.89
3.IPSM	95.91	11.51	113.69	12.39	5.69**	1.17
4.ISQ	70.15	12.53	102.85	14.34	9.34**	1.72
5.SAIS:Insecure	31.54	13.49	45.65	13.72	3.96**	.81
6.SAIS:Secure	34.18	6.89	23.11	12.11	-4.16**	.96
7.SBS	21.00	7.62	34.81	9.81	6.09**	1.23

Table 3.7. Depressed and Control Groups differed significantly on all social rank questionnaires, with Depressed scoring higher on all measures except the Secure SAIS subscale

Perfectionism

Independent samples t-tests found the Depressed group had significantly higher scores than Controls for both Self-Orientated Perfectionism (t(60)= 2.32, p=.024), and Socially-Prescribed Perfectionism (t(60) 2.03, p=.047), but not for Other-Orientated Perfectionism (Table 3.8).

	Controls		*Depressed*			
Measure	*M*	*SD*	*M*	*SD*	t statistic	*d*
Self-Orientated	61.30	13.70	70.35	16.23	-2.320*	.79
Other-Orientated	55.24	11.59	55.33	15.49	-0.027	.01
Socially-Prescribed	52.36	13.59	59.53	14.47	-2.027*	.77

Table 3.8. Depressed and Control Groups differed significantly on two of the three perfectionism subscales. * correlation is significant at the 0.05 level

Across the whole sample, Self-Orientated and Socially-Prescribed Perfectionism correlated with all 6 measures of the social rank questionnaires, while Other-Orientated Perfectionism only correlated with the insecure subscale of the SAIS (r(60)=.39, *p*=.002). The SAIS insecure subscale had the strongest correlations with all three dimensions of perfectionism (Table 3.9).

Measure	*Self-Orientated*	*Other-Orientated*	*Socially-Prescribed*
1.BAI	.26*	-.10	.29*
2.BDI-II	.34**	.05	.31*
3.IPSM	.31*	.09	.30*
4.ISQ	.32*	.13	.32*
5.SAIS:Insecure	.56**	.39**	.51**
6.SAIS:Secure	-.47**	-.23	-.45**
7.SBS	.32*	.13	.35**

Table 3.9. Self-Orientated and Socially-Prescribed perfectionism were found to correlate with all measures of the social rank questionnaires. ** indicates *p*<.01, *indicates *p*<.05

3. 5. DISCUSSION

This chapter presented an overview of the task protocol and general methods in this thesis, including study design, measures and tasks used, recruitment procedures and ethical

considerations. We also characterised the differences in affective and social processing between groups in our participant sample, replicating previous findings that Depression involves systemic social processing biases using a series of self-report measures. Our Depressed sample showed significantly higher scores than controls on all measures of maladaptive social functioning, while significant relationships were found both within and across groups between measures of affect and social functioning.

Social Rank and Mood Questionnaires

The findings of this analysis validated the distinction between the Control and Depressed groups utilised in this thesis on the basis of symptom severity. Our results identified significant group differences on the BDI-II and BAI, with the Control group scoring within the minimal range of the BDI-II, and the Depressed group scoring at the upper end of the moderate range. These findings replicate previous results supporting the reliability of the BDI-II (Wang & Gorenstein, 2013) and BAI (Lee, Kim & Cho, 2018) in discriminating clinical and non-clinical subjects, and validate their use for screening in the general population.

Moreover, these findings support the existence of a relationship between symptom severity and systemic biases in social processing in Depression; we found that across groups, both the BDI-II and BAI correlated strongly (to the $p<0.01$ level) with all social rank questionnaires, including involuntary subordination, submissive behaviour, interpersonal sensitivity and striving to avoid inferiority. The Social Risk Hypothesis of Depressed Mood (SRH; Allen & Badcock, 2003) conceptualises submissiveness as a defensive behavioural strategy that emerges in response to perceptions of inferiority and prolonged involuntary subordination and predicts heightened interpersonal sensitivity to avert social risks. Our findings align well with these predictions, and with previous literature which has associated social processing biases

with rumination (Cheung, Gilbert & Irons, 2004) self-harm (Gilbert et al., 2010) and self-criticism (Sturman & Mongrain, 2010).

Perfectionism

Perfectionism was included in the current analysis as an indicator of sensitivity to interpersonal discrepancies (Socially-Prescribed Perfectionism) and intrapersonal discrepancies (Self-Orientated Perfectionism). These discrepancies are relevant within the broader context of the thesis, which is informed by social homeostatic theories whereby self-esteem, and the associated affective experience, function to return us to our 'set-point', our ideal rank or self. These discrepancies are considered in greater detail in the Actual-Ideal Task (Chapter 4) and Social Feedback Task (Chapter 5) chapters.

Of the three dimensions of perfectionism, previous literature indicates that Socially-Prescribed Perfectionism (SPP) is the strongest predictor of Depression, and shows the most correlations with measures of social status and submissiveness (Wyatt & Gilbert, 1998). The results presented here provide mixed support for these findings. We found that both SPP and Self-Orientated Perfectionism (SOP) differed significantly between groups, and both had significant correlations with all measures of the affective and social processing questionnaires, aligning with previous findings relating perfectionism with affect, submissiveness, and social anxiety (Nepon, Flett, Hewitt & Molnar, 2011). Perfectionistic individuals are thought to be more prone to involuntary subordination because they are more likely to perceive defeat and less able to accept defeat following setbacks (Sturman & Mongrain, 2008), while the SRH views depressed mood as an adaptive response to prolonged involuntary subordination. Our findings indicate that both SOP and SPP are related to social processing and affect.

Overall, our depressed sample was found to show greater interpersonal sensitivity, in addition to heightened submissive behaviours and involuntary subordination while striving to avoid

inferiority. These findings support the predictions of the SRH in relation to social processing in Depression. We also found preliminary evidence that Socially-Prescribed and Self-Orientated perfectionism correlate with measures of both depressed affect and social rank. Finally, this chapter outlined the overall protocol for this thesis. The protocol involves a group behavioural session on Day One, which participants completed in groups of five of the same clinical status, followed by a scanning session on Day Two. Participants completed five tasks across the two sessions; the Actual Ideal Task (Chapter 4) and Social Feedback Task (Chapter 5), designed to investigate neural processing of discrepancy and the hypothesis that Depression is associated with heightened sensitivity to such discrepancies, and the Ultimatum Game (Chapter 6), Public Goods Game (Chapter 7) and Balloon Analogue Risk Task (Chapter 8), designed to assess social behaviours in the context of the hypotheses of the SRH. The participant sample described in this chapter remains the same across tasks, with any variations detailed in their respective chapters.

CHAPTER 4. NEURAL PROCESSING OF DISCREPANCIES BETWEEN ACTUAL AND IDEAL SELF-CONCEPTS

4.1. INTRODUCTION

According to the Social Risk Hypothesis of Depressed Mood (SRH; Allen & Badcock, 2003), many features of depressed mood can be understood as mechanisms by which to reduce the social risk of exclusion. This theory necessitates a system for the monitoring of our social rank, which is achieved via evaluations of our Social Investment Potential (SIP), the ratio between our perceived social burden and social value to the group. In Chapter 1, we discussed how SIP might be determined through monitoring of social signals of rejection and inclusion, and the concept that humans have evolved mental mechanisms that attempt to maintain their SIP around an ideal value, a self-evaluative set-point where there is a balance between comfortably providing positive value to the group, while also maximising the returns from one's social investments. Thus, we might expect that an individual's evaluations of themselves against this self-standard will be an important feature in determining affective and social processing, providing potential insight into why otherwise successful people, for example in terms of socioeconomic status or other external factors, still suffer from Depression (Freeman et al., 2016). This chapter explores the presence of discrepancies between actual and desired self-concepts in samples of healthy controls and individuals with Depression and investigates the overlap between neural regions associated with self-discrepancy and social status.

Self-Discrepancy and Mood

Self-Discrepancy Theory (Higgins, 1987) proposes that individuals have two different dimensions of self-beliefs, self-standpoints and self-domains, and that discrepancies between these representations leads to specific emotional vulnerabilities. Self-standpoints refer to the perspective from which the individual is evaluated, being their own or a significant other. Self-domains refer to concepts of the self, and include an Actual self-concept, how you perceive yourself to be in reality, an Ideal self-concept, a representation of your hopes and aspirations

for yourself, and an Ought self-concept, representations of your responsibilities and obligations. Higgins (1987) theorised that discrepancies from the Ought-self represent a potential for negative outcomes, conferring agitation-related feelings, whereas discrepancies from the Ideal-self represent the absence of positive outcomes, leading to feelings of dejection and dissatisfaction. Accordingly, while discrepancies between Ought and Actual selves have been associated with anxiety (Strauman & Higgins, 1988) and eating disorders (Vartanian, 2012), discrepancies between Ideal and Actual selves have been widely related to both diagnoses of Major Depressive Disorder (MDD) and subclinical negative affect (Johns & Peters, 2012; Strauman, 1989).

Actual-Ideal discrepancies, where the Actual self is perceived as falling short of the standards of the Ideal self, have been associated with general symptoms of negative affect, such as feeling discouraged or sad, as well as being associated with the endorsement of symptoms of MDD (Bruch, Rivet & Laurenti, 2000), and negatively associated with self-assurance and joviality (Barnett, Moore & Harp, 2017). Actual-Ideal self-discrepancies have also been associated with lower self-esteem and self- worth (Renaud & McConnell, 2006; Moretti & Higgins, 1990) and self-discrepancies have been found to explain individual differences in self-esteem beyond that explained by measuresof affect (Barnett & Womack, 2015). According to SRH, self-esteem is the conscious experience of our Social Investment Potential (SIP); thus, we might hypothesise that perceptions of our Actual self, relative to our Ideal-self contribute to evaluation of our SIP (Allen and Badcock, 2003).

Within a clinical setting, reductions in depressive symptoms following cognitive therapy have been associated with reductions in Actual-Ideal discrepancies (Watson, Bryan & Thrash, 2014). Furthermore, investigations including remitted MDD participants find that they report larger Actual-Ideal discrepancies than never-depressed controls, but fewer than those experiencing a current episode of MDD (Fairbrother & Moretti, 1998). Finally, the relationship between depression and Actual-Ideal discrepancies has been demonstrated cross-culturally (Gürcan-Yıldırım & Gençöz, 2020).

The higher occurrence of self-discrepancies in depression may be related to the absence of the self-enhancement bias usually observed in never-depressed subjects, sometimes termed depressive realism (Alloy & Abramson, 1979). Healthy participants have been shown to make unrealistically positive evaluations regarding their performance relative to others (Wolpe, Wolpert & Rowe, 2014) the likelihood of future events (Lench & Bench, 2012) and their self-concepts (Dunning, 2005). In comparison, depressed participants make more accurate but less optimistic evaluations of the likelihood of experiencing adverse life events (Korn et al., 2014) and about the controllability of uncontrollable events (Alloy & Abramson, 1979). Importantly, this relative accuracy may extend to perceptions of the self and others. Edison and Adams (1992) had depressed and control subjects engage in dyadic interactions, which were then rated by themselves and an objective coder on measures of non-verbal social behaviour, social skill, appropriateness of statements and level of social comfort. Depressed subjects' self-ratings *and* partner-ratings were more closely correlated with the objective coder's rating than those of healthy controls. Interestingly, studies which have compared judgements of the self with judgements of others have found that depressed participants display a positive bias when rating others' performance that is not seen in controls (Moore & Fresco, 2012).

Several models have attempted to bridge the relationship between self-discrepancies and affect by suggesting that emotion functions to signal discrepancies from a goal or reference point, and to motivate self-regulatory processes which move oneself towards that point (See Higgins (1998) and Well & Matthews (1994) for examples). From a social evolutionary standpoint, Sociometer Theory (Leary & Baumeister, 2000) posits that self-esteem varies with perceived social inclusion and eligibility for significant relationships, and that the negative affective component of low self-esteem motivates individuals to engage in corrective action to maintain minimum levels of social regard. Monitoring and evaluating social cues in this way is too cognitively demanding to be processed consciously, therefore the sociometer operates unconsciously and continuously, similar to other human feedback systems designed to maintain homeostasis. This parallels the idea of social burden and social value in the SRH (Allen & Badcock, 2003), and we can conceptualise Ideal Self-Concepts as a cognitive representation of an individual's social homeostatic set-point, with the emotional response to self-discrepancy functioning as an automatic signal of the need to return to that point.

Neuroimaging Research on Self-Discrepancies

The concept of "Social Homeostasis" now underlies a growing body of imaging research which seeks to identify a neural system, or systems, able to monitor social conditions, detectdeviations from a set-point, and activate compensatory mechanisms (Matthews & Tye, 2019).The 'neural sociometer' has previously been associated with elevated levels of activation in the dorsal anterior cingulate cortex (dACC) and anterior insula (AI) (Eisenberger et al., 2011), regions' associated with social rejection and social acceptance (Eisenberger, Lieberman & Williams, 2003; Dalgleish et al., 2017). See Chapter 1 for a more detailed review. The mentalizing network also presents potential regions of interest; this network seems to underliethe ability to make inferences about the mental states of others (Frith & Frith, 2006) and is based around the medial prefrontal cortex (mPFC), superior temporal sulcus (STS) and

tempoparietal junction (TPJ) (Frith & Frith,2003). Previous findings suggest that self-referential processing may overlap with aspects of social cognition in regions of this network (Mitchell, Banaji & Macrae, 2005; Lombardo et al., 2010). A meta-analysis of this literature found that judgements of the self and others (relative to non-mentalizing judgements) were associated with greater activation in the mPFC, left TPJ and posterior cingulate, while judgements of the self (relative to judgements of others) were associated with greater ventral mPFC and left insula activation (Denny, Kober, Wager & Ochsner, 2012). With particular relevance to the current task, activation in this network has been found to vary with social status while engaging in tasks involving the processing of social information, with greater activation in the mPFC, dorsal mPFC and precuneus associated with lower self-reported social status (Muscatell et al., 2012).

However, there is limited existing neuroimaging literature relating specifically to Actual-Ideal discrepancies. Eddington et al. (2009) investigated Actual-Ideal discrepancies within the context of Regulatory Focus Theory (Higgins, 1998), which characterises the pursuit of ones Ideal-self as a promotion goal. Adjectives that participants reported as being representative of their “Ideal” but not “Actual” self were used as primes for promotion goals and presented to participants incidentally during a depth of processing task while in the MRI scanner. They found that these onsets were associated with significant attenuations in baseline activity in the left orbitofrontal cortex (OFC) of depressed participants relative to healthy controls.

The only previous study identified as specifically addressing activation during contemplation of Actual-Ideal discrepancies was conducted by Shi et al. (2016). In this study, healthy participants with different putative genetic susceptibilities to mental health problems were presented with trait adjectives and asked to indicate how far the Actual self was from the Ideal self in terms of that trait. Greater Actual-Ideal self-discrepancies were associated with increased activity in the dACC and left AI, as well as in the dorsal striatum – regions previously

associated with a desire for external rewards (Wilson et al., 2005) – and the dorsal mPFC – a region proposed to be involved in the down-regulation of emotion during reward cravings (Kober et al., 2010). As far as we are aware there have been no studies examining the neural correlates of Actual-Ideal discrepancies in individuals with Depression or at risk of Depression. The current task therefore utilised a similar protocol to Shi et al., (2016) replicating the design across with groups of never-depressed and in-episode depressed participants.

Hypotheses

We predicted that depressed individuals would report larger discrepancies than Controls between their Actual and Ideal self-concepts, and that across the sample, the number of large discrepancies would correlate with severity of depressive symptoms.

We predicted that in trials where participants reported a discrepancy between their Actual and Ideal self-concepts, we would observe greater activation in regions associated with monitoring of social evaluation, including the dorsal anterior cingulate cortex (dACC) and anterior insula (AI). Based on the SRH, we predicted that the Depressed group would exhibit greater activation in these regions during large discrepancies relative to the Control group, due to the hypothesised sensitivity to discrepancy in this group.

4.2. METHOD

Participants

Full details of participant demographics, exclusion criteria and recruitment procedures can be found in Chapter 3. Two participants from the Depressed group and four from the Control group were excluded due to image acquisition difficulties, three participants from the Depressed group and three from the Control group were excluded due to failure to provide ratings for 4+ trials, indicating lack of engagement in the task. The participant sample was

therefore 50 adults (28 female, age range 18-64, mean=44.74 yrs) recruited from the MRC CBU volunteer panel. There were 25 never-depressed Control participants (13 female, age range 18-64, mean=42.15yrs) and 25 Depressed participants (15 female, age range 21-64, mean=48.11yrs). There were no significant differences between the groups in relation to gender ($X^2(1, N=50)=.05$, $p=.82$) or age ($t(48)=-1.50$, $p=.14$). The Depressed group had an average Beck Depression Inventory II (BDI-II) score of 25.45, falling within the moderate range (20-28), which was significantly different to the Control average of 6.27 ($t(48)=8.32$, $p<.001$).

Protocol

This task formed part of a larger protocol, detailed in Chapter 3. Relevant to the current task, on Day 1, participants completed several mood and social rank questionnaires, and rated themselves on a range of trait adjectives. On Day 2, participants completed a functional magnetic resonance imaging scan (fMRI) which involved reflecting on and rating the discrepancies between their concepts of Actual-Self and Ideal-Self.

Questionnaires

At the beginning of the behavioural testing session participants completed questionnaires related to mood and subjective social functioning (full details in Chapter 3). Two were included in the analysis of the current task; the Beck Depression Inventory II (BDI-II; Beck, Steer & Brown, 1996) was included as a measure of affect, while both the Socially-Prescribed and Self-Orientated subscales of the Hewitt-Flett Multidimensional Perfectionism Scale (MPS; Hewitt & Flett, 1990) were included as measures of tolerance for self-discrepancy. The Socially-Prescribed subscale (items 5, 9, 11, 13, 18, 21, 25, 30, 31, 33, 35, 37, 39, 41, 44) assesses an individual's tendency to believe that others expect perfection from them, while the Self-Orientated subscale (items 1, 6, 8, 12, 14, 15, 17, 20, 23, 28, 32, 34, 36, 40, 42) assesses the

tendency to set high standards and beliefs about the importance of attaining perfection (Appendix 3.14). Full details of both measures can be found in Chapter 3.

Actual-Self: Rating Trait Characteristics

During the behavioural testing session, participants completed a Self-Ratings sheet. The purpose of this sheet was to familiarise participants with the concept of an Actual-Self and encourage self-reflection in preparation for the scanning session. Participants were instructed to reflect on how they viewed themselves to be in reality, then rated this Actual-Self on 24 positive and 24 negative trait adjectives, on a 1-10 Likert scale where 1 indicated "Not like me" and 10 indicated "Very much like me". These trait adjectives had been derived from a larger pool of 142 traits as those which were the most or least socially desirable (for full detailson trait word selection see Chapter 3).

Actual-Ideal Discrepancy Ratings

The scanning protocol for this study was based on an earlier investigation by Shi et al. (2016). During the scanning session participants performed Actual/Ideal self-discrepancy judgements on the 48 trait adjectives they had previously rated. Participants first viewed a 20-second information screen, which encouraged them to bring to mind their Actual and Ideal self-concepts and explained the use of the button box for rating discrepancies. 48 adjectives were presented, 24 positive, 24 negative, each for a duration of 6 seconds, followed by a 1 second fixation slide (Figure 4.1). The adjectives were presented in the centre of the screen with a four-point scale below. The scale ranged from 1 "Very Close" to 4 "Very Far" and participants indicated the distance between their Actual and Ideal self-concepts by moving the slider along the scale using a button-box.

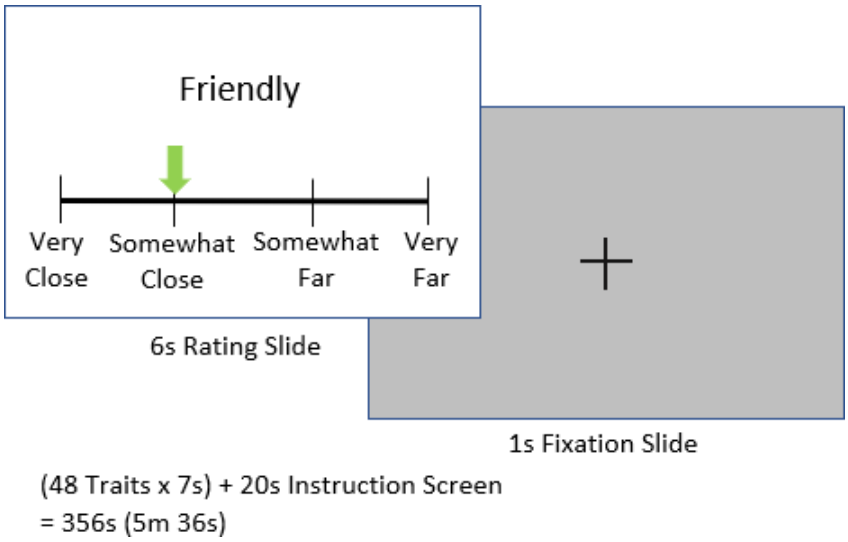


Figure 4.1. Slides and timings sequence for one trait adjective as it appeared to participants in the scanner. Participants saw 48 adjectives and used a button box to respond.

Data Analysis

An average discrepancy rating was computed for each participant by converting the ratings onto a 1-4 scale (Very Close, 1; Somewhat Close, 2; Somewhat Far, 3; Very Far, 4), thereby accounting for the relationship between the number of each type of rating (i.e. fewer of one type of categorical rating would mean more of other types). An independent groups t-test was then run between groups to identify differences in the size of reported discrepancies. A Pearson correlation was run between this variable and BDI score across groups, to investigate a relationship with symptom severity.

Imaging Analysis

Image pre-processing details are reported in Chapter 3. We corrected for multiple comparisons using a cluster-wise Family-wise error (FWE) threshold of 0.05, using an initial cluster-defining height threshold of $p<0.001$ uncorrected with a *k* cluster extent threshold of 202 voxels (https://zenodo.org/record/1689891#.YUrhE33TU2w). We approached the whole-brain

imaging analysis in two ways. First, asking which neural regions respond to larger or smaller sizes of discrepancy using a parametric modulation of discrepancy size. Secondly, we applied a binary approach focusing on activation differences between small discrepancies and large discrepancies. Small discrepancies were trials in which participants provided a “Very Close” and “Somewhat Close” rating. Large discrepancies were trials in which participants provided a “Somewhat Far” and “Very Far” rating. These trials were combined to create a Small Discrepancy and Large Discrepancy contrasts, respectively.

For the parametric modulation, at the first level, individual participant files were run with all trials in one condition, and the size of the discrepancy (1 (Small Discrepancy) – 4 (Large Discrepancy) was entered as a parametric modulator, creating two contrasts for the effect of larger and smaller size of discrepancy. At the second level, these contrasts were entered into one-sample (within-group) and independent (between-group) sample t-tests.

For the binary analysis, to identify differences in neural processing between trials with Large and Small discrepancies, a separate first level analysis was conducted with 2 conditions based on trial type, Small Discrepancy (“Very Close” and “Somewhat Close” ratings) and Large Discrepancy (“Somewhat Far” and “Very Far” ratings) and generated 4 contrasts; Small Discrepancy, Large Discrepancy, Small>Large and Large>Small subtraction contrasts. To identify a main effect of self-discrepancy, a one-way repeated measures ANOVA was run across groups at the second level. A Factorial ANOVA with two factors of Group (Depressed/Control) and Discrepancy (Small/Large) was run to identify differences between groups.

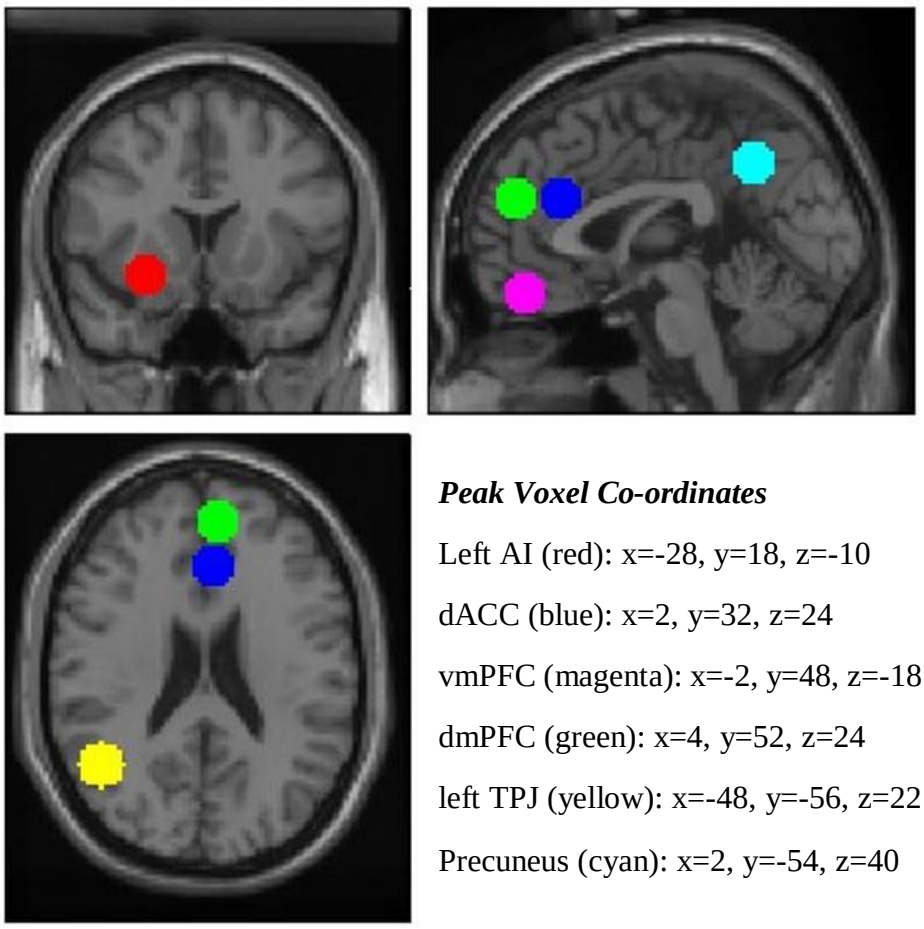
Individual differences

Regressions were run against three questionnaire covariates: scores on the Beck Depression Inventory-II (BDI-II) and on both the Socially-Prescribed and Self-Orientated subscales of the MPS.

Region of Interest (ROI) Analysis

Finally, we analysed the effect of discrepancy in a set of six predetermined ROIs, run using MarsBar in SPM8 (Figure 4.2). ROIs were the dACC and AI regions, as identified by Dalgleish et al. (2017) as the key social evaluation centres (dACC peak voxel x=2, y=32, z=24, left AI peak voxel x=-28, y=18, z=-10), as well as four key regions of the mentalizing network. A search for "Mentalizing" on Neurosynth (www.neurosynth.org) produced 124 studies.

Peak voxel co-ordinates for the dorsomedial Pre Frontal Cortex (dmPFC), ventromedial PFC, Left Temporoparietal Junction (TPJ) and Precuneus were all taken from this map and used to produce 10mm spheres which formed the ROIs (dmPFC x=4/y=52/z=24; vmPFC x=-2/y=48/z=-18; Left TPJ x=-48/y=-56/z=22; Precuneus x=2/y=-54/z=40). These ROIs were run against the increasing discrepancy contrast, the Large vs Small Discrepancy contrasts within and across groups, and the covariate measures during Large Discrepancies. All ROI analyses were corrected for multiple comparisons using Bonferroni correction.



Peak Voxel Co-ordinates

Left AI (red): x=-28, y=18, z=-10

dACC (blue): x=2, y=32, z=24

vmPFC (magenta): x=-2, y=48, z=-18

dmPFC (green): x=4, y=52, z=24

left TPJ (yellow): x=-48, y=-56, z=22

Precuneus (cyan): x=2, y=-54, z=40

Figure 4.2. Peak Voxel Co-ordinates for 6 Regions of Interest, including the left Anterior Insula and dorsal Anterior Cingulate Cortex, as well as regions of the mentalizing network

4.3. RESULTS

Behavioural

In line with our predictions, there was a significant difference between the average discrepancy size reported by Depressed participants compared to Controls ($t(46)=2.62$, $p=.012$, $d=.74$), although the correlation with BDI score across groups did not reach significance ($r(46)=.27$, $p=.068$). Figure 4.3 displays the frequency of each rating by group.

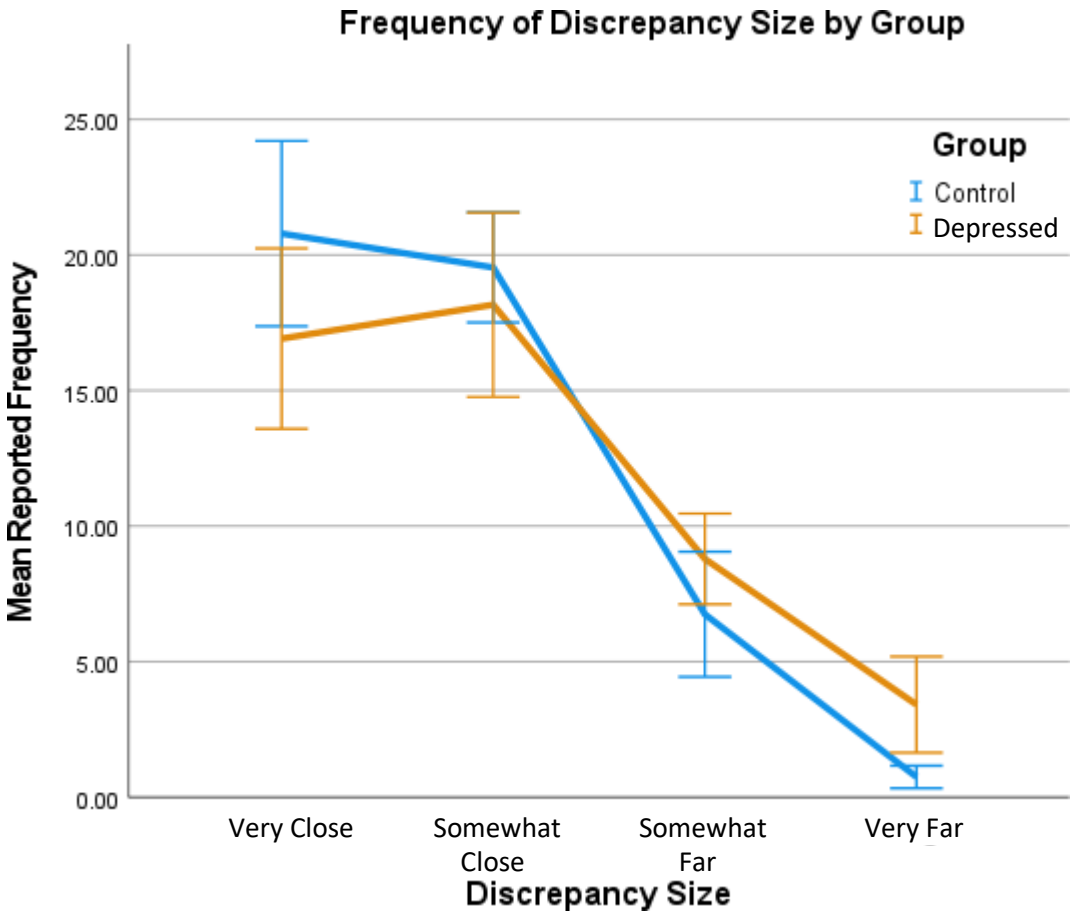


Figure 4.3. Frequency of Discrepancy Sizes by Group. The Depressed Group reported a higher average discrepancy size than Controls.

Imaging

Parametric Analysis

The parametric analysis found no regions significantly associated with increasing discrepancy either across or within groups.

Binary Analysis: Small vs Large Discrepancies

A Factorial ANOVA with two factors of Group (Depressed/Control) and Discrepancy (Small/Large) was run (Table 4.1). A main effect of group was observed in two clusters around

the bilateral middle and posterior cingulate gyrus, and left putamen, caudate and anterior insula, with greater activation in the Depressed group (Figure 4.4A). There was no interaction between Group and Discrepancy, no Main Effect of Discrepancy Type, and no significant activations or deactivations associated with the between-groups contrasts.

Region	**k**	**Z value**	***Cluster-Level p***	**MNI Co-ordinates**		
				x	*y*	*z*
Main Effect of Group (Depressed>Controls)						
Middle Cingulate Gyrus, Posterior Cingulate Gyrus	1051	4.87	0.000	4	-22	26
Left Putamen, Caudate and Anterior Insula	412	4.60	0.001	-22	20	0

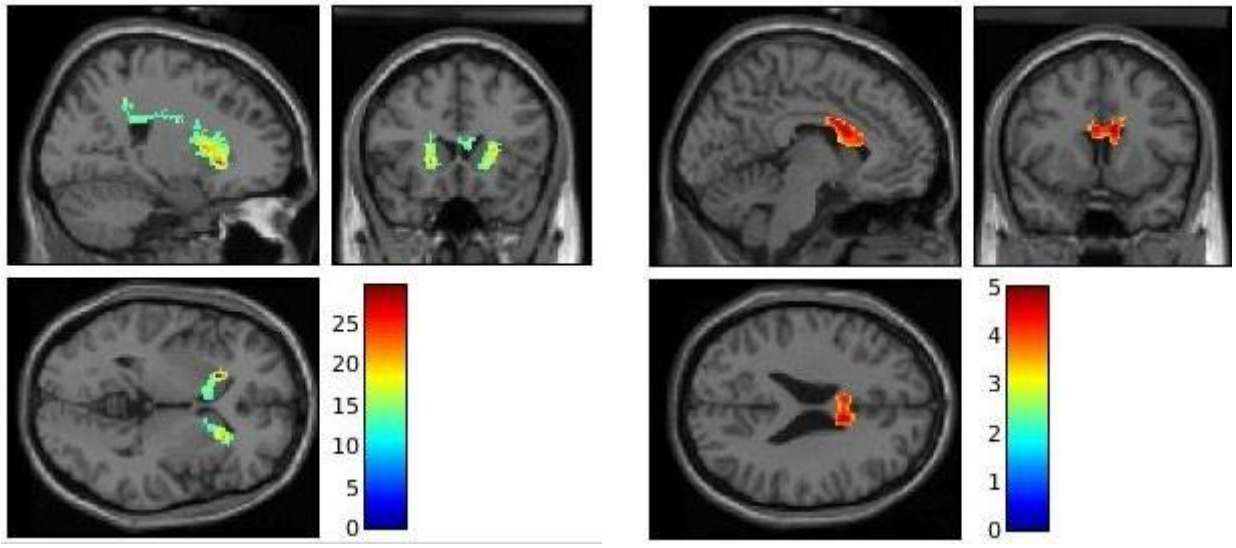
Table 4.1. Results of the Factorial ANOVA reporting Cluster-Level p values showing a main effect of Clinical Group.

ROI analyses

The ROI analysis did not find significant activations associated with any of our planned contrasts. Full data is presented in Appendix 4.1.

Covariates

One-way ANCOVAs were run between the Large over Small Discrepancy contrast and scores on three covariate measures, the BDI, Self-Perfectionism and Social Perfectionism scales, both across and within groups (Table 4.2). At the whole brain level, across groups, increasing BDI was associated with a cluster of activation in the right middle cingulate gyrus (Figure 4.4B).



(A) (B)

Figure 4.4. A) A Main effect of Group was observed in the left putamen, caudate and anterior insula, which showed increased activation in the Depressed Group. B) In the Large over Small Discrepancy contrast, increasing BDI was associated with increased activation in the middle cingulate gyrus.

Region	**k**	**Z value**	***Cluster-level p***	**MNI Co-ordinates**		
				x	**y**	**z**
Across Groups						
Increasing BDI						
Right Middle Cingulate Gyrus	553	4.36	0.000	6	10	24

Table 4.2. Results of One-Way ANCOVAs between covariate measures and Large>Small Discrepancy Contrast

An ROI analysis was run using these contrasts, which found that in Depressed participants, activation in the vmPFC correlated with increasing BDI score, while activation in the dACC and left AI was significantly associated with increasing Self Perfectionism (Table 4.3).

	Contrast Value	T Statistic	Corrected P
Depressed			
Increasing Self Perfectionism			
dACC	0.02	3.09	0.018943
Left AI	0.01	3.19	0.015159
Increasing BDI			
vmPFC	0.01	2.86	0.041663

Table 4.3. Results of ROI analysis between covariate measures and Large>Small Discrepancy contrast

4.4. DISCUSSION

Previous literature has presented compelling evidence that depressed individuals perceive large discrepancies between their Actual and Ideal self-concepts (Barnett, Moore & Harp, 2017). Theoretical models have linked this to self-regulatory and homeostatic mechanisms where affect functions to motivate behaviours which return the individual to their set-point (Higgins, 1998). In this study, we examined the presence of self-discrepancies in depressed and healthy control samples and performed exploratory neuroimaging analyses utilising a protocol from Shi et al. (2016). Behavioural data supported our prediction that the Depressed group would report larger discrepancies between their Actual and Ideal selves. At the neural level, the data revealed that increasing BDI score was associated with activations in the posterior and midcingulate gyrus (at the whole brain level) and vmPFC (at the ROI level) during Large relative to Small discrepancies; previous literature has suggested a role for the vmPFC in the emotional component of self-referential processing (Wang et al., 2012; Zhu et al., 2007), while the posterior cingulate cortex has been implicated in studies of self-referential processing (Yoshimura et al., 2009). The ROI analysis also identified in the dorsal anterior cingulate cortex (dACC) and left anterior insula (AI) in relation to increasing self-perfectionism during Large relative to Small discrepancies; as previously discussed, these

regions are associated with social evaluation (Dalgleish et al., 2017), and may form the basis of an automatic neural system for monitoring social status. These findings provide evidence that reflection on self-discrepancies recruits a more complex network than previously outlined, involving regions implicated in social and emotional processing, and which may vary with depressive symptoms.

Regions of the Default Mode Network

The Default Mode Network (DMN) consists of bilateral cortical areas in the medial prefrontal, medial and lateral parietal, and medial and lateral temporal cortices of the brain, that are conceptualised to represent a baseline mode of brain function that is suspended during goal-directed behaviours, seen as deactivation (Raichle et al., 2001). The DMN is subdivided into three major regions; the dorsal medial prefrontal cortex, the ventral medial prefrontal cortex and the posterior cingulate cortex and adjacent precuneus (Raichle, 2015). Disrupted connectivity and activation in these subsystems has been observed previously in Depression (Sambataro et al., 2013).

Ventral Medial Prefrontal Cortex

ROI analyses of the Large over Small discrepancy contrast found that activation in the ventromedial prefrontal cortex (vmPFC) was associated with increasing BDI score in the Depressed group. The anatomical connectivity of this area is well-documented, and places it within a network of regions which convey sensory external information to structures such as the hypothalamus and amygdala, representing an important link between external cues, social behaviour, and mood (Ongur & Price, 2000; Raichle, 2015). The medial prefrontal cortex has been associated with self-referential processing, being identified during judgements of the self-relevance of trait adjectives (Macrae et al., 2004; Kelley et al., 2002). A meta-analysis from Van der Meer, Costafreda, Aleman and David (2010) subsequently distinguished the

roles of the dmPFC and vmPFC, with the vmPFC being responsible for the affective component of self-referential processing, and the dmPFC responsible for distinguishing self vs other relevant information. This characterisation of the regions is supported by a psychophysiological interaction study from Schmitz and Johnson (2006) which observed two dissociable networks during self-appraisal; a vmPFC-paralimbic 'affective' pathway, and a dmPFC-cortical-hippocampal 'cognitive' pathway. Accordingly, the vmPFC has a well-established role in the downregulation of negative affect; a meta-analysis by Yang, Tsai and Li (2020) of affective studies reporting concurrent amygdala and vmPFC activation found that hyperactivation of the vmPFC was associated with diminished right amygdala activity during regulation of negative emotions. Conversely, lesioning of the vmPFC is associated with elevated amygdala activity in response to negative aversive stimuli (Motzkin et al., 2014).

However, studies of the vmPFC in the context of the DMN have found that a lack of deactivation is indicative of negative affect. Sheline et al. (2009) found that Depressed participants exhibited a failure to deactivate the vmPFC during negative stimuli, in both passive observation and active reappraisal conditions. Similarly, Simpson et al (2001) found that deactivation of the vmPFC was inversely correlated to reported anxiety during task performance, such that those participants with highest anxiety exhibited the least deactivation. This has been linked to the role of the DMN in self-referential processing, indicating disordered negative self-referential thoughts in Depression. Our observation that vmPFC activation correlated with BDI score during the Large over Small discrepancy contrast might indicate greater self-referential processing during large discrepancies in the Depressed group.

Middle and Posterior Cingulate Gyri

The data observed a significant Main Effect of Group in the posterior and middle cingulate gyri, which were also associated with increasing BDI score during the Large over Small discrepancy contrast across groups. The posterior region of the cingulate cortex (PCC) has been associated previously with contemplation of personal goals (Spreng, Stevens, Chamberlain, Gilmore, & Schacter, 2010) and is consistently implicated in studies of self-referential processing (Yoshimura et al., 2009; Northoff and Bermpohl, 2004). In view of this, findings which have indicated dysfunction in this region of the DMN in Depression have been interpreted as a possible basis of ruminative tendencies (Li et al., 2017). This relationship was investigated by Cooney et al. (2010) who contrasted trials involving self-rumination with abstract and concrete thinking distractor conditions. They found that the depressed sample exhibited hyperactivity in the PCC during the rumination condition, compared to controls or distraction conditions. Discrepancies between Actual and Ideal self-concepts have previously been associated with rumination behaviourally; in an investigation by Roelofs et al. (2007) of Papageorgiou and Wells (2003) non-clinical metacognitive model of rumination and Depression, structural equation modelling found that, in addition to a direct link with Depression, self-discrepancies showed an indirect effect on Depression via metacognitions and rumination, and an association with positive beliefs about rumination. Our finding, that the Depressed group exhibited greater PCC activity during the self-reflection task, aligns with this previous literature indicating dysfunction in regions of the default mode network involved in self-referential processing in individuals with depressive symptoms.

Implications for Sociometer Theory

dACC and Anterior Insula

The ROI analysis identified the dACC and left AI associated with increasing self-perfectionism in the Large over No Discrepancy contrast in the Depressed group. These findings could support the idea that the dACC-AI acts as a kind of neural alarm system for negative social information (Eisenberger et al., 2011) and that, in line with the SRH, this system is hyperactive in individuals with Depression and perfectionism. There is limited existing evidence regarding the neural correlates of perfectionism, however several studies have identified the dACC as a possible region (Wu et al., 2017; Geisler et al., 2017). This may be linked to the well-documented role of the dACC in error-detection (Botvinick, Cohen, & Carter, 2004), as errors are thought to be particularly salient for perfectionists because they optimize future behaviour (Barke et al., 2017). In the context of the SRH, optimizing one's self-perception is crucial to correctly estimating SIP, thereby enabling the individual to maximise their return on social investments. Previous theories have conceptualised self-discrepancies as triggers for self-regulatory mechanisms (Higgins, 1998; Wells and Matthews, 1984); our findings indicate that the dACC and AI are more active during reflection on such discrepancies in perfectionistic individuals, possibly indicating greater error-monitoring or negative affect.

An alternative interpretation is that our results reflect the involvement of the dACC in conflict monitoring (Shackman et al., 2011) and management of cognitive dissonance (Wang et al., 2016), which may be relevant during reflection on large discrepancies which require monitoring of the conflict between the wish to achieve the Ideal self and awareness of the discrepancy.

Regions of the Dorsal Striatum

Shi et al. (2016) found activation in the dorsal medial prefrontal cortex (dmPFC), bilateral dStr and left ventral striatum associated with self-discrepancies. Although the current study

did not relate activation in these regions specifically with larger discrepancies, the data showed that greater activation was observed in the right putamen and caudate in the Depressed group across the task. These findings are in line with previous research which has identified increased activation and connectivity of the dorsal striatum in Depression (Gabbay et al., 2013; Kerestes et al., 2014). Shi et al. (2016) found the left lateralised striatum was particularly associated with individuals' reported perceived importance of possessing Ideal traits, and therefore interpreted activation in this region in the context of previous literature which has found the dStr involved in the desire for external rewards (Kober et al., 2010). Our findings may indicate that the importance and desire to possess Ideal traits is heightened during Depression. This interpretation is in line with Leary and Baumeister's Sociometer theory, in which they utilise the concept of satiation to describe how an individual's drive to achieve social desirability will subside as they approach their optimum level. Notably, the traits in this paradigm were previously identified as being highly socially relevant, conferring high social value or social undesirability. We can therefore tentatively interpret our findings in the context of the SRH as resulting from the heightened importance of obtaining socially desirable traits, and increasing or maintaining ones SIP, in Depression.

Limitations and Future Directions

A limitation of the current study is that participants were not asked to rate the subjective personal importance of each trait word; Trait words with greater relevance to one's self-concept would be more salient during this task and are likely to elicit stronger emotional responses. Accordingly, previous evidence suggests that the perceived self-relevance of trait words moderates activation in regions of the medial prefrontal cortex (Moran et al., 2006). In Shi et al.s study (2016) participants reported the importance of possessing trait words, and this was found to be positively predicted by left striatal activity. A second limitation in the design may have been the scale that participants used to indicate the size of discrepancy for

each trait word. This scale was replicated from Shi et al., and ran from 1-4, with 1 indicating "Very Close" (to my Ideal self) and 4 indicating "Very Far". Using the same scale for both positively and negatively valenced trait words was not intuitive for participants; a large discrepancy from a positive trait indicates that you have less than your desired level of that trait (e.g., Kindness) whereas a large discrepancy from a negative trait indicates you are more than your desired level (e.g., Hostile). This was identified during piloting of the task, and the experimenter's script was updated to include a verbal test of participants understanding. The scale itself was not altered, in order to faithfully replicate Shi et al.s design, however, future research might benefit from a two-directional scale, with no-discrepancy as the central point.

A third possible limitation is that this study only tested one cultural sample. Social cognitive processes, including construal of the self, have been found to vary across cultural contexts (Markus & Kitayama, 2010). This may result from the influence of context on our perceptions of others and their behaviour (Han et al., 2013) or from differing cultural emphasis on self-concepts that are either independent, defining oneself on one's uniqueness and individualism, or interdependent, based on belongingness and group membership (Marcus & Kitayama, 1991). Research suggests that these differences are evident at a neural level; during judgements of the relevance of trait adjectives to the self, the subjects' mother, and a public figure, Chinese subjects display a significant overlap in activation of the mPFC during self and mother conditions, compared to unique activation in the self-condition in Western subjects (Zhu, Zhang, Fan and Han, 2007). Moreover, self-reflection on social attributes has been found to differentially activate the temporoparietal junction in collectivist cultures (Ma et al., 2014). Future research may therefore benefit from cross-cultural validation of findings regarding self-discrepancy.

Future research might also consider the role of discrepancies between ones Actual and Ought selves. The current study considered only Ideal selves due to their relationship with

Depression (Johns & Peters, 2012) and self-esteem (Renaud & McConnell, 2006). Regulatory Focus Theory (Higgins, 1998) conceptualises Ideal and Ought selves as representing different motivational states; Ideal selves represent an approach goal, with the desired end-state as the reference point, while Ought selves represent an avoidance goal, in which the reference point is an undesired end-state. Homeostatic theories align more closely with the idea of balancing one's social value and burden around an Ideal set-point, however, Ought selves often include social norms and beliefs about others' expectations (Sun & Guo, 2014), and may therefore be a good candidate for representing this set point in a social context, or for defining when discrepancies from this point have reached a critical level.

The Socio-evolutionary theories of affect considered in this thesis, including the Social Risk Hypothesis of Depressed Mood, conceptualise discrepancy from a set-point as a key trigger for adaptive behavioural mechanisms. The current study therefore aimed to investigate the presence of intrapersonal discrepancies between ones actual and ideal self-concepts in depressed individuals, and perform exploratory neuroimaging analysis of discrepancy related regions. We found that the Depressed group reported more large discrepancies between Ideal and Actual self-concepts. Perfectionism was found to correlate with activity in the dACC and left AI during large discrepancies in our Depressed group; in the context of these regions' associations with social evaluation (Dalgleish et al., 2017) our findings may support a role for the dACC-AI in integrating internal evaluations of one's social value relative to an ideal point with external social feedback. Our findings also contribute to the existing literature suggesting that dysfunction in subsystems of the Default Mode Network may underlie ruminative or negative emotional self-referential processing in Depression. More work investigating the neural basis of discrepancies in self-concepts is needed and should include the Ought-self.

CHAPTER 5. NEURAL PROCESSING OF DISCREPANT SOCIAL FEEDBACK

5.1. INTRODUCTION

The Social Risk Hypothesis of Depressed Mood (SRH; Allen & Badcock, 2003) posits that depressed mood emerged as an adaptive response to critically low social rank, which functions to mitigate the risk of social exclusion through various behavioural mechanisms. Chapter 1 discussed how these mechanisms are triggered when the ratio between an individual's social value and social burden has fallen too low, implying that one's objective social position may be less salient than their position relative to an ideal homeostatic 'set-point'. Leary and Baumeister (2000) proposed the existence of a "Sociometer", which tracks social experiences to monitor our position within a group and integrate this knowledge into computations of our self-esteem. The current task therefore had two aims; firstly, to investigate the neural regions that might constitute a Sociometer through presentation of rank-discrepant feedback, and secondly, to investigate differences in neural activation in depressed participants relative to healthy controls, in response to rank-discrepant feedback.

This first aim was addressed in Chapter 2, using data from Dalgleish et al. (2017), however participants could only receive feedback of 'winner', 'loser', or one of two 'middle' positions, meaning that distinguishing discrepancy in terms of rank from the positive or negative valence of the feedback was challenging. The current study addressed this by providing feedback across a 10-point scale; for example, if an individual rated themself as 2 out of 10, and subsequently received feedback that they were a 3 out of 10, this would be positive relative to their self-rating, despite being a relatively poor (negative) overall score. This study also built on the Chapter 2 reanalysis by including a depressed sample, allowing us to address our second aim relating to the SRH.

The Sociometer

Leary and Baumeister (2000) proposed the existence of a "Sociometer", a construct which tracks both rejection and inclusion experiences and integrates them into the felt sensation of self-esteem, which provides an indicator of our felt degree of social inclusion and an emotional motivation for corrective behavioural mechanisms. This conceptualisation of self-esteemaligns with the well-established relationship between self-esteem and perceptions of social acceptance (Denissen et al., 2008) and social rejection (Bernstein et al., 2013). Moreover, depression is reliably related to low self-esteem (see meta-analysis from Sowislo & Orth, 2013), and both self-esteem and depression can be predicted by social connectedness (Williams & Galliher, 2006). Sociometer theory and its relationship with the SRH are discussed in greaterdetail in Chapter 1, therefore the current chapter will focus on mentalizing and pain processingbrain regions which may represent a neural matrix for this system.

Neural Signature of Social Pain

Existing literature has identified the dorsal anterior cingulate cortex (dACC) and anterior insula (AI) as potential neural correlates of this sociometer (Eisenberger et al., 2011). Previously, the dACC has been associated with conflict monitoring (Botvinick, 2001), salience (Perini et al., 2018) and error detection (Hyman et al., 2013), however, a large-scale reverse inference fMRI analysis found that the best psychological description of dACC function was in relation to pain processing (Lieberman and Eisenberger, 2015). The anterior insula (AI), has also been related to physical pain, including anticipation of pain (Lutz et al., 2013), and the perception of pain in others (Koban et al., 2013). Eisenberger (2012) theorised that physical pain processing regions may have been co-opted during human evolution to increase the salience of social exclusion. This is relevant in the context of the sociometer, which should be sensitive to interpersonal experiences which communicate status relevant information, including

experiences of social rejection, or social pain. Several studies have shown dACC and AI activation in relation to social pain, including rejection during ball-tossing games (Eisenberger, Lieberman & Williams, 2003), negative social judgements (Eisenberger, Inagaki, Muscatell, Byrne-Haltom & Leary, 2011) and romantic breakups (Kross et al., 2011). This pain-based account was expanded recently in line with sociometer theory to include signals of inclusivity, with studies finding these regions activated comparably in response to both positive and negative social feedback (Achterberg et al., 2016; Dalgleish et al., 2017).

Low Mood and the Sociometer

In depression, the SRH predicts that the sociometer should be more sensitive to signals of social risk, as an adaptive measure. Previous studies have supported the idea that this matrix is more active in depression, although this has more frequently been in relation to rejection feedback (Yttregahl et al., 2018; Silk et al., 2013; Onoda et al., 2010). In a task which involved receiving rejecting, accepting or neutral feedback from self-selected romantic partners, participants with depression showed increased activity in the right AI during rejection relative to neutral feedback. Moreover, activation in the dACC was higher in the Depression group than the Control group during rejection trials (Yttregahl et al., 2018). A simulated “Chatroom” style task, in which participants could be accepted or rejected from conversations, found that adolescents with depression exhibited greater activation in response to rejection in the left AI, bilateral amygdala, subgenual ACC and left nucleus accumbens when compared to controls (Silk et al., 2013). There is also literature examining this matrix in relation to poor self-esteem more broadly; during a Cyberball game – a computerised ball-tossing task – participants with low trait self-esteem experienced more social pain in relation to rejection (being left out of the ball toss by the two other players) than those with high trait self-esteem, which correlated with greater activation in the dACC (Onoda et al., 2010).

Mentalizing Regions

The term mentalizing refers to the process by which we make inferences about the mental states of others, allowing us to make predictions about their behaviour which can guide our interactions (Frith & Frith, 2006). Previous research has consistently indicated the temporal poles, medial prefrontal cortex (mPFC), superior temporal sulcus (STS) and tempoparietal junction (TPJ) in this process (Frith & Frith, 2003). Research into the relationship between self-esteem, mood and social feedback has implicated regions of this network; a study in which participants received feedback from peers after a social interaction found that activity in the mPFC, TPJ, inferior frontal gyrus and STS correlated with the discrepancy between one's own self-rating and the feedback they received (Korn et al., 2012). More positive feedback was also associated with mPFC activation, and this activation predicted positive updates when participants were subsequently asked to re-rate themselves. The mPFC was also identified by Yang et al. (2016) who found that trait self-esteem was associated with activation in the mPFC, posterior cingulate and occipital cortices during evaluation of positive social feedback. In another study, Schie et al. (2018) found that low self-esteem was related to decreased activation during positive feedback in the mPFC, insula, anterior cingulate cortex (ACC) and posterior cingulate cortex (PCC). Negative feedback was related to activation in the bilateral AI, caudate nucleus and ACC. The study also had participants rate how applicable they felt feedback was to themselves; they found that positive feedback that was rated as highly applicable was associated with reduced TPJ activation, another mentalising region, possibly due to the regions role in other-referential processing (Schurz et al., 2014).

Demographic Feedback

Festinger's (1954) original theory of social comparison posits that individuals evaluate their opinions and abilities by comparing themselves with people who are similar on relevant dimensions. This has subsequently been developed to include a self-enhancement function for social comparison, through favourable downward-comparisons, and discounting comparisons

with higher groups (Wills, 1981), mechanisms both affected in depression (Buunk & Brenninkmeyer, 2000). Hounkpatin and Wetherall (2014) found that depressed individuals exhibited greater symptom severity when their income ranked low within their social or demographic comparison groups, such as age group or gender, and rank of income was better able to predict depressive symptoms than models which considered income utility or distance from the mean income. This finding is supported by a similar study which found that the relationship between absolute income and lifetime suicidal thoughts and attempts could be accounted for by income rank within all social comparison groups (Wetherall et al., 2015). These findings may indicate that individuals are more sensitive to their position within the context of their group, perhaps because they are lessable to discount differences on the basis of demographic identity.

Beach and Tesser (2000) relate this to evolutionary theory by expanding on the work of Leary and Downs (1995), which suggested that self-esteem acts as an affective sociometer, rooted in our concern about being excluded by others. Beach and Tesser point out that "*we are not equally concerned with being excluded by all people and all groups*" and suggested that psychological closeness to others amplifies the effect of social consequences to our self-esteem. Therefore, there are both evolutionary and cognitive mechanisms for why affect seems to be more greatly impacted by comparison with similar groups.

The current task used a novel methodology whereby participants received feedback about their ratings relative to four of their demographic groups: Age, Gender, Education and Occupation. Control group participants received this demographic feedback in addition to feedback from a group of fellow participants, while the depression group only received the demographic feedback.

Hypotheses

Based on previous literature, our first hypothesis was that there is a unified region forprocessing social-rank relevant information, which is focused in the AI and dACC. Our first prediction was therefore that the degree of discrepancy of social-rank feedback would correlate with activations in socially relevant neural regions including the dACC and AI. Our first analysis tested this prediction by comparing socially discrepant and non-discrepant feedback in the Control sample (the only sample to receive social feedback).

Our second hypothesis, based on the SRH, was that our depression group would show greater neural sensitivity to rank-relevant information and discrepancies. We therefore predicted that depressed individuals would show greater AI and dACC activation than Controls, and that this might correlate with measures of submissiveness and sensitivity to social rank. We tested this by comparing Depressed and Control participants neural responses to differently valenced feedback. A secondary prediction based on this hypothesis was that activation in these areas might correlate with questionnaire measures relevant to feelings of inferiority and subordination.

As the use of demographic feedback is a novel methodology, we carried out a final analysis comparing the response of Control participants to demographic and social feedback, for which there was no directional hypothesis.

5.2. METHOD

Participants

Full details of participant demographics, exclusion criteria and recruitment procedures can be found in Chapter 3. Participants were 62 adults (38 female, range 18-74, mean=45.77yrs)

recruited from the MRC CBU volunteer panel. To summarise, this comprised a Control group of 32 participants (20 female, age range 18-64, mean=44.85yrs) and 30 participants with Depression (18 female, age range 21-74, mean=47.44yrs). The Depressed group had an average BDI score of 27.61, within the moderate range (20-28), which was significantly different to the Control average of 5.45 ($t(38)=9.674, p<.001$). There were no significant differences between the groups in relation to gender ($X^2(1, N=62)=.027$, $p=.87$), age ($t(60)=-.75$, $p=.46$), education level ($X^2(1, N=62)=4.48$, $p=.34$) or ethnicity ($X^2(1, N=62)=7.77$, $p=.10$).

Protocol

This task formed part of a larger protocol carried out over two days (detailed in Chapter 3). Relevant to the current task, on the first day, participants completed affective and social-rank questionnaires, in addition to rating themselves and their fellow participants (after spending time together) on a range of socially relevant attributes. All of the tasks during this session involved interactions between participants, so each was assigned a Player Number to identify whom they were communicating with. On the second day, participants completed a functional Magnetic Resonance Imaging (fMRI) session, which involved viewing the feedback they had received from their groupmates, as well as feedback based on a “Demographic Questionnaire” (detailed below).

Questionnaires

At the beginning of the behavioural testing session participants completed questionnaires related to mood and social rank, full details of which can be found in Chapter 3. Three of these measures were included in the analysis of the current task; the Beck Depression Inventory-II (BDI; Beck, Steer & Brown, 1996) was included as a measure of affect, while the Striving to Avoid Inferiority Scale (SAIS; Gilbert, Broomhead, Irons & McEwan, 2007) and Involuntary Subordination Questionnaire (ISQ; Sturman, 2011) were included as measures of behaviour

relevant to social rank. These measures were chosen as they specifically address feelings of social inferiority which might be prompted by the feedback design of the current task.

Demographic Comparison Measure

During the behavioural testing session on the first day, participants were given a questionnaire titled "Demographic Comparison Questionnaire" (Appendix 5.1). Participants were informed that the questionnaire had been administered by several research groups across the UK, and completed by hundreds of people, thereby allowing us to compare their results with that of specific demographic groups with a high degree of validity.

In fact, this questionnaire was the two unrelated questionnaires which was administered in this way to create believability for the subsequent scanning task. For ethical reasons, this protocol did not involve depressed participants receiving feedback from their groupmates. Instead, a Demographic Condition was created, in which participants received feedback relating to their rank on a range of attributes relative to others of the same gender, education level, occupation, or age. This feedback was supposedly calculated from the "Demographic Comparison Questionnaire" but was in fact manipulated by the experimenters to ensure an equal distribution of positive and negatively valenced discrepancies, that were comparable across participants. This condition was completed by both Control and Depressed groups.

Self and Other Ratings

The final step of the behavioural protocol was the Self and Others Ratings Sheet (Appendix 5.2). The first part of the sheet listed 20 socially relevant trait adjectives, 10 negative and 10 positive, and had participants rate to what extent each adjective described them on a Likert scale from 1 to 10, where 1 indicated "Not at All" and 10 indicated "Very Much So". Full details of how these adjectives were selected and validated is included in Chapter 3. The purpose of this portion of the sheet was to gather participants' ratings of themselves, to

calculate any discrepancy from the feedback they would subsequently receive in the scanner. The second part of the sheet asked participants to rate each of their groupmates on 10 of the socially relevant trait adjectives, using the same scale. After completing the sheet the Control subjects were told that they would see the others' ratings of them during scanning. The purpose of this portion of the sheet was to create believability for the scanning task.

Imaging Session

Full details of the image preprocessing protocol are detailed in Chapter 3. Participants viewed their ratings in the scanner. Control participants completed both the demographic and social feedback conditions, while Depressed participants completed only the demographic condition. Runs for both conditions started with a 10-second information screen, informing participants of how the task would progress. Each condition contained feedback relevant to 10 trait adjectives. Each trait adjective was addressed within its own feedback epoch, and each epoch comprised three components (Figure 5.1). First was a 5-second Self-Rating reminder slide, which presented the adjective they were being rated on during this epoch and their self-rating from the previous day. Following a 3-second fixation period, the second component was the feedback itself; participants viewed four feedback slides of 3.5-seconds each, separated with a jittered fixation slide of 1-5s duration. In the social condition, each feedback slide displayed the trait adjective being assessed, the numerical identifier of the group member who had provided the rating (i.e. Player 3), and their rating of the participant out of 10 for this adjective. In the demographic condition, each feedback slide displayed the trait adjective being assessed, the demographic group the player was being compared with (i.e. Age group), and the questionnaire rating of them, adjusted for the group average. Following another 3-second fixation period, the third and final component was an 8-second Re-rating slide, in which participants could choose to adjust their self-rating up or down the 10-point scale using a button box.

The feedback received by participants in both conditions was experimentally manipulated to ensure a range of discrepancy sizes and directions across adjectives of both valences (20 Positive and 20 Negatively valenced slides across a total of 40 in each condition). Accordingly, participants completed a believability questionnaire after scanning to identify any disbelief in the validity of the feedback (Appendix 5.3). Finally, participants were fully debriefed on the manipulation of feedback, and received an information sheet to this effect (Appendix 3.6).

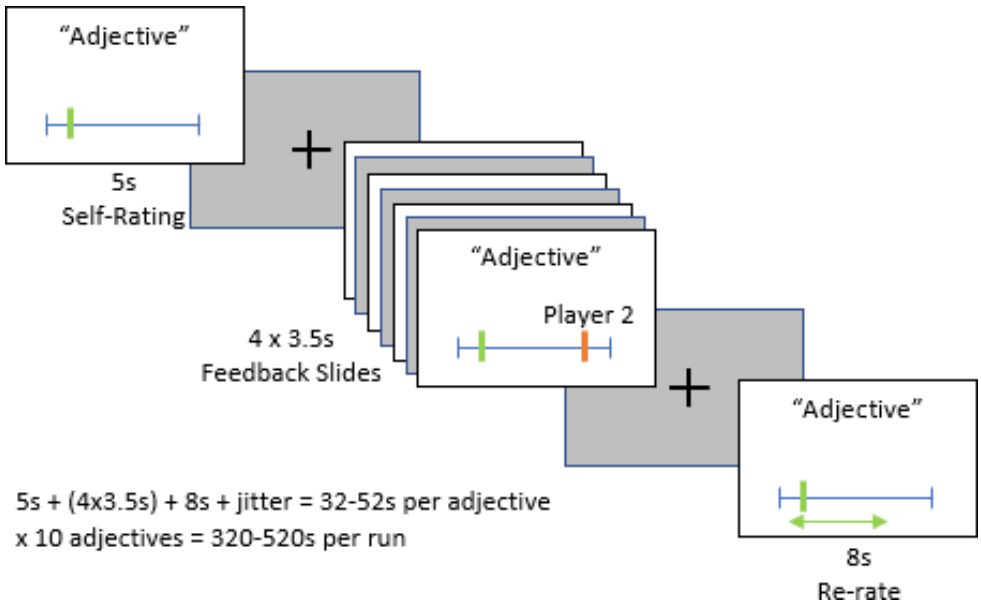


Figure 5.1. Slides and timings sequence for one adjective as it appeared to participants in the scanner. Each run contained 10 sequences, for each of 10 adjectives. Controls completed two runs, once for demographic and once for social feedback, Depressed participants completed one run for demographic feedback only.

Data Analysis

Image preprocessing was conducted as described in Chapter 3. We corrected for multiple comparisons using a cluster-wise Family-wise error (FWE) threshold of 0.05, using an initial cluster-defining height threshold of $p<0.001$ uncorrected with a *k* cluster extent threshold of 200 voxels (https://zenodo.org/record/1689891#.YUrhE33TU2w).

Social Rank Discrepancies

Our first prediction was that the degree of discrepancy of social-rank feedback would correlate with activations in socially relevant neural regions including the dACC and AI. The social feedback condition was only carried out by the Control group, so the following analysis is limited to this sample. To test our prediction, one-sample t-tests were carried out to establish differences in activated voxels during Positive Discrepancy, Negative Discrepancy and No Discrepancy Trials, at the whole brain level. These were binary contrasts; Positive Discrepancy was defined as receiving a higher rating (than your self-rating) on a socially positive trait or receiving a lower rating (than your self-rating) on a socially negative trait. For example, a higher rating on 'Trustworthy' and a lower rating on 'Rude' would both be categorised as Positive Discrepancies. The opposite pattern was used to define Negative Discrepancies. Batch files were created for each participant individually, within which trials were organised into these three conditions, and the following contrasts were generated; 'Positive Over Negative', 'Positive Over None', 'Negative Over Positive', 'Negative Over None', 'Both Over None'. To reduce the number of comparisons in the analysis, a one-way, repeated measures ANOVA was then run between Positive, Negative and No Discrepancy Trials, using the same contrasts as the initial one-way t-tests.

A follow up analysis was conducted to analyse the effect of discrepancy, irrespective of valence. Batch files were created for each participant individually, in which all trials were combined into a single condition. The relative discrepancy of the feedback received during each trial was introduced as a parametric modulator, using a quadratic polynomial expansion; this allowed us to investigate activations associated with large discrepancies (of both positive and negative valence) compared with small discrepancies (of both positive and negative valence).

We next analysed the effect of discrepancy in a set of six predetermined ROIs, run using MarsBar in SPM8. ROIs were the dACC and AI regions, as identified by Dalgleish et al. (2017) as the key social "pain and gain" centres (dACC peak voxel x=2, y=32, z=24, left AI peak voxel x=-28, y=18, z=-10), as well as four key regions of the mentalizing network. A search for "Mentalizing" on Neurosynth (www.neurosynth.org) produced 124 studies. Peak voxel co-ordinates for the dmPFC, vmPFC, Left TPJ and Precuneus were all taken from this map and used to produce 10mm spheres which formed the ROIs (dmPFC x=4/y=52/z=24; vmPFC x=-2/y=48/z=-18; Left TPJ x=-48/y=-56/z=22; Precuneus x=2/y=-54/z=40). These ROIs were run against Positive Discrepancy, Negative Discrepancy and No Discrepancy conditions.

Finally, regressions were run against four questionnaire covariates: the Secure and Insecure subscales of the Striving to Avoid Inferiority Scale (SAIS), the Beck Depression Inventory (BDI) and the Involuntary Subordination Questionnaire (ISQ). Batch files were created and run against these covariates for the five contrasts outlined above.

Depression and Rank Feedback

Our second prediction was that activation relating to rank feedback would be greater in the Depressed group compared to Controls. For ethical reasons, the Depressed group only completed the demographic feedback condition of the task, so the following analysis only considers this condition. To test our prediction, we first analysed the effect of discrepancy and valence within the Depressed and Control groups separately, and then considered differences between the groups.

The Within-Groups analyses were carried out in a similar way to those outlined above; One-sample t-tests were carried out to establish differences during Positive Discrepancy, Negative Discrepancy and No Discrepancy Trials, followed by a one-way, repeated measures ANOVA. Both tests used the following contrasts; 'Positive Over Negative', 'Positive Over None',

‘Negative Over Positive’, ‘Negative Over None’, ‘Both Over None’. The six ROIs (dACC, left AI, dmPFC, vmPFC, TPJ and Precuneus) and same four questionnaire covariates were run against these contrasts.

For the Between-Groups analysis, a full-factorial ANOVA was run with two factors, Group and Discrepancy Type. The Group factor had two levels, Control and Depressed, while the Discrepancy Type factor had three levels, Positive, Negative and No Discrepancy. Contrasts were run comparing the groups on each of the three levels.

Demographic VS Social Feedback

Demographic Feedback has rarely been used previously to investigate social rank. Our final analysis was therefore a non-directional and exploratory investigation into differences in response to Social and Demographic Feedback types. This analysis was limited to the Control Group, as the only group which completed both conditions.

A full-factorial ANOVA was run with two factors; Feedback Type and Discrepancy Type. Feedback Type had two levels, Social or Demographic, while Discrepancy Type had three levels, Positive, Negative and No Discrepancy. This analysis was run using the individual participant files generated in the previous analyses. Contrasts were run to compare discrepancy types across valences.

5.3. RESULTS

Social Feedback Condition

Social Feedback was only received by the Control group. Whole-brain data found the right posterior insula was significantly deactivated in the BothDiscrepancies>NoDiscrepancy contrast (Table 5.1). Figure 5.2 shows deactivations of the right posterior insula across Positive,

Negative and No Discrepancy Conditions. No significant activations were found for any of the other contrasts. The parametric analysis found that increasing negative discrepancy was associated with activation in the right middle cingulate gyrus (Table 5.1). No activations were associated with increasing positive discrepancy.

Region			***Cluster-***	**MNI coordinates**		
	k	**Z value**	***Level p***	*x*	*y*	*z*
BothDiscrepancy>NoDiscrepancy						
Right Posterior Insula	216	4.04	0.007	48	0	-4
Increasing Negative Discrepancy						
Right Middle Cingulate Gyrus	676	4.33	0.000	8	16	24

Table 5.1. Results of the One-Way ANOVA and Parametric Analysis.

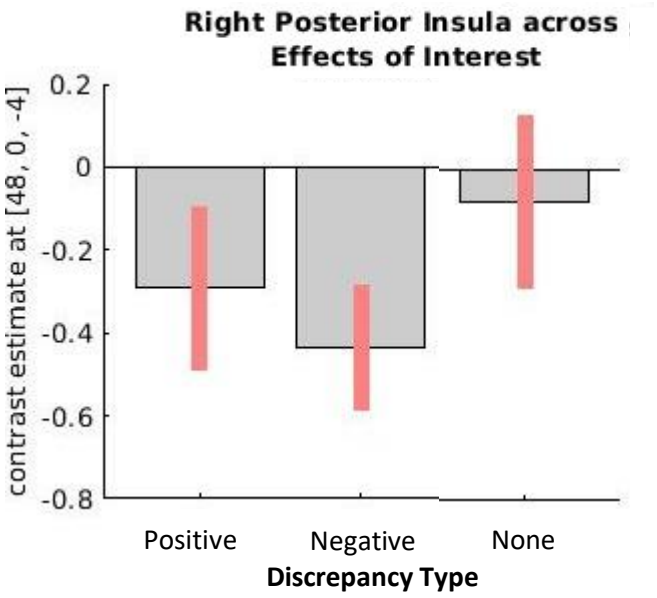


Figure 5.2. Contrast Estimate Plot for Right Posterior Insula across Effects of Interest. Deactivation was significantly reduced during No Discrepancy trials.

The covariate analysis did not find any relationships significant at the FWE level, and none of the six ROIs showed significant activations (Appendix 5.4).

Demographic Feedback Condition

Within Groups

The Demographic Feedback condition was completed by both the Depressed and Control groups. In the Depressed Group, a Repeated Measures ANOVA found a significant deactivation during Positive>No Discrepancy trials in the Right Posterior and Anterior Insula (Table 5.2). In the Control Group, the ANOVA found a significant activation in the left middle temporal gyrus during Negative>No Discrepancy trials (Table 5.2).

Region	k	Z value	*Cluster-Level p*	MNI coordinates		
				x	*y*	*z*
Depressed: Positive > No Discrepancy						
Deactivation						
Right Insula	344	5.68	0.000	52	-6	0
Controls : Negative > No Discrepancy						
Activation						
Left middle temporal gyrus	713	4.90	0.000	-58	-52	8

Table 5.2. Results of the Demographic Condition Repeated Measures ANOVAs within groups.

ROI analyses of the Demographic Feedback condition (Table 5.3) found that deactivation of the dACC (MNI x=2, y=32, x=24) was associated with Positive Discrepancies in the Control Group (t=2.43, p=.0483) and with both Positive and Negative Discrepancies in the Depressed Group (Positive; t=2.61, p=.0302, Negative; t=2.78, p=.0189), although there were no significant interactions between groups. Full ROI data are presented in Appendix 5.5.

	Contrast Value	T statistic	Corrected p
Depressed			
Positive Discrepancy: Deactivation			
dACC	-0.23	2.61	0.030278
Negative Discrepancy: Deactivation			
dACC	-0.22	2.78	0.018966
Controls			
Positive Discrepancy: Deactivation			
dACC	-0.21	2.43	0.04836

Table 5.3. ROI analyses of the Demographic Condition found significant deactivations in the dACC in both Depressed and Control Subjects.

No significant regions were found to be associated with the covariate analysis.

Between Groups

The between-groups ANOVA of the demographic feedback found a significant positive main effect of Group in the left lingual gyrus and right precentral gyrus (Table 5.4). These regions were deactivated in the Depressed group relative to Controls; Figure 5.3 shows activation of the right precentral gyrus across the effects of interest. There were no significant interactions between group and discrepancy type or between the individual contrasts.

Region	**k**	**Z value**	***Cluster-Level p***	**MNI coordinates**		
				x	*y*	*z*
Main Effect of Group: Depressed>Controls						
Left Lingual Gyrus	426	4.65	0.001	-14	-54	-8
Right Precentral Gyrus	205	4.25	0.024	38	-16	64

Table 5.4. Results of the Demographic Condition Factorial ANOVA.

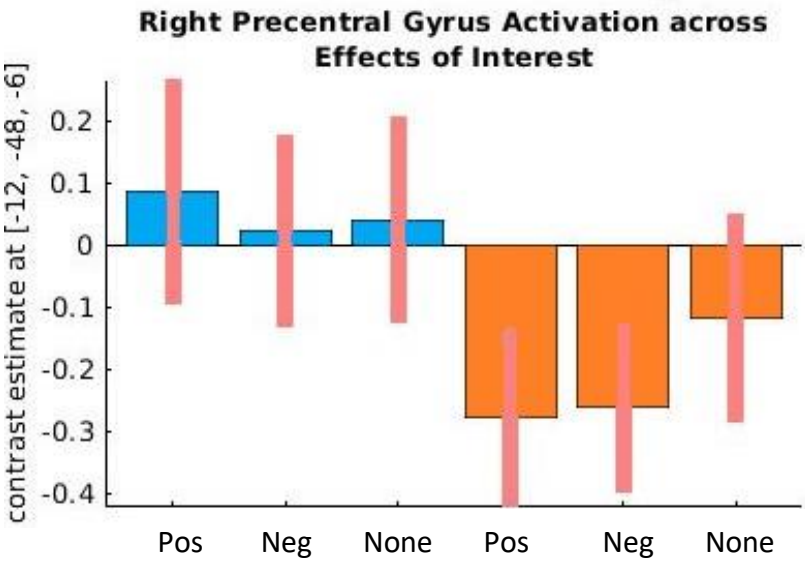


Figure 5.3. Contrast Estimate Plot for the Right Precentral Gyrus across Effects of Interest. The Depressed group exhibited greater deactivation relative to Controls across valences

Demographic vs Social Feedback – Controls Only

The results of the Feedback Condition Factorial ANOVA are shown in Table 5.5. There was a main effect of Condition (Social/Demographic) in the Precuneus, which was driven by deactivation in the Social Condition. When both positively and negatively valenced discrepancies were pooled, the Social Condition relative to the Demographic condition produced a significant cluster of activation in the Right Entorhinal Area and Amygdala.

Region	**k**	**Z value**	***Cluster-Level p***	**MNI coordinates**		
				x	*y*	*z*
Main Effect of Condition: Social>Demographic						
Deactivation						
Right Precuneus	277	4.65	0.006	12	-70	30
Social Discrepancies > Demographic Discrepancies						
Activation						
Right Entorhinal Area, Amygdala, Anterior Insula	260	4.35	0.016	28	4	-24

Table 5.5. Results of the Demographic vs Social Condition Factorial ANOVA.

5.4. DISCUSSION

The current task had two hypotheses; firstly, that there exists a neural index for processing social-rank relevant information, and secondly, and that this index is *more* active in response to social feedback in Depression. Based on previous literature, we predicted that this would be focused in the anterior insula (AI) and dorsal anterior cingulate cortex (dACC). This prediction was not supported, as our ROI analyses found that the dACC was *deactivated* in the Depressed group during both positive and negative discrepancies., while the Control group showed deactivation of the dACC during positive discrepancies only. The whole-brain analysis found the anterior and posterior insula deactivated in the Control group during both positive and negative discrepancies, but deactivated uniquely during positive discrepancies in the Depressed group. Alongside these findings, we observed increased activation in response to negative discrepancies, compared to no discrepancy trials, in the left middle temporal gyrus, and activation in the middle cingulate gyrus associated with increasing negativity of discrepancy.

The Sociometer Matrix

We found that the dACC was deactivated in the Depressed group during both positive and negative discrepancies, and for positive discrepancies only in Controls. These findings were unexpected in the context of our hypotheses regarding depression and the sociometer and are in contrast with previous research which has implicated the dACC as a core region in the processing of painful social feedback (Rotge et al., 2015).

Similar findings were reported previously by Hooley et al. (2009), who found that patients in remission from depression showed deactivation of the dACC in response to hearing maternal criticism. One potential explanation for the patterns observed in this task is the dACC's association with cognitive and emotional control and reappraisal; evidence suggests that the

dACC is involved in the selection and application of reappraisal strategies in relation to negative emotions (Ochsner & Gross, 2005). Inhibition of negative affect is associated with activation in the dACC (Phan et al., 2005) and BOLD responses in the dACC are predictive of success in employing cognitive reappraisal techniques (Ochsner et al., 2002). Stronger connectivity of the dACC with prefrontal cortices has been found in individuals with high reappraisal skills such as experienced meditators (Brewer et al., 2011). This function might explain why the dACC was less active specifically in positive discrepancies in Controls, due to the lack of need to reappraise any negative emotions, but less active in both positive and negative discrepancies in the Depressed group, perhaps indicating poor directional emotional control and reappraisal skills in response to social feedback, a feature reported previously in depressed subjects (Joorman & Siemer, 2013).

At the whole brain level, the right posterior insula (rPI) was deactivated in Control participants during discrepant as opposed to non-discrepant trials in the social condition, irrespective of valence, while in Depressed participants, the rPI and right anterior insula (rAI) were deactivated only in positively discrepant relative to no-discrepant trials. While this does not align with our predictions regarding the sociometer, it might be understood in relation to coding of self-relevant emotional information. A study from Perini et al. (2018), which manipulated self-salience and feedback type, found evidence of AI and PI involvement in processing of self-relevant information, and argued that this provides a stronger explanation for its activation during social feedback than pain-based accounts. Similarly, a study investigating the overlap of self-salience and emotion, by having participants rate the extent of self-relatedness of emotionally salient pictures, found high self-relevance was associated with activation in the anterior insula in addition to cortical midline structures (Phan et al., 2004). Cabanis et al. (2013) performed a study in which participants read sentences describing positive or negative social situations and decided whether the situation was caused by themselves or others. They found

that negative situations that participants attributed to themselves were associated with activation in the anterior insula bilaterally. Therefore, the AI may be involved in the processing of self-relevant emotional information, including social feedback. The posterior insula is involved in somatosensory and interoceptive function (Kuehn et al., 2016) and processing of somatosensory pain (Segerdahl et al., 2019). Much like the anterior insula, it has also been associated with the social component of these sensory experiences, for example viewing others being touched in caring manner elicits activation in the posterior insula (Morrison et al., 2011), while viewing images of a previous romantic partner following an unwanted break-up elicits the same (Kross et al, 2011).

In the absence of significant interactions, we can only draw tentative interpretations regarding particular groups, which might form a basis for further investigation. The observed deactivation of the AI in Controls during discrepant trials might be indicative of low perceived self-relevance, in line with well-established positive and confirmatory self-biases in healthy populations (Alicke & Govorun, 2005) particularly as deactivation was greatest in response to negative feedback. Conversely, in Depressed participants, deactivation exclusively during positive discrepancies might be indicative of low perceived self-relevance for positive social feedback, which aligns with evidence that the positive self-judgement bias is reduced in Depression (Dunn et al., 2009). These findings are not without precedent, as a previous study from Schie et al. (2018) found that individuals with low self-esteem showed decreased activation in the insula during positive feedback. This kind of selective treatment of self-relevant information can have a significant impact on the development of self-beliefs (Sharot & Garrett, 2016); our findings might therefore be best interpreted as preliminary evidence that mechanisms which might preserve self-esteem, such as attributions of self-relevance and emotional control, are altered in social contexts in Depression.

Alternatively, there are possible methodological explanations for these results; Firstly, this study used a novel feedback protocol in which participants received demographic feedback on ratings out of 10. In contrast, a large proportion of the current social rejection literature has utilised the Cyberball task (Williams, 2001); a meta-analysis of Cyberball tasks from Cacioppo et al. (2013) found evidence that dACC activation may be greater in Cyberball compared to other tasks, which might in-part explain why our results are so different from much of the literature. Secondly, the time course of the study may have impacted our results; previously, Dedovic et al. (2016) found that repeated bouts of feedback led to decreases in dACC activity in healthy participants, and similarly, Moor (2012) found dACC activity was lower during repeated Cyberball sessions. In the current task, Control participants completed the two feedback conditions one after the other, meaning the repetition may have influenced the patterns observed in the dACC.

Increasingly Negative Discrepant Feedback

In Controls, two regions were identified as being associated with negative discrepant feedback; the middle cingulate gyrus was associated with increasing negativity of discrepancy, while the left middle temporal gyrus (MTg) was associated with the negative over no discrepancy contrast, both at the whole brain level. The MTg has an established relationship with various emotion regulation strategies; Modinos, Ormel and Aleman (2010) found that reappraisal of negative stimuli was associated with MTg activation, while Goldin et al. (2008) found emotional suppression during negative emotion-eliciting films was also associated with the MTg. The activations observed in this task might suggest that this region is also involved in the regulation of emotions resulting from negative social feedback. It is worth noting that this activation was not observed in the Depressed group, reminiscent of a meta-analysis of studies involving cognitive reappraisal in mood and anxiety disorders, which found that the MTg consistently showed higher activation in Controls relative to patients during negative

reappraisals (Pico-Perez et al., 2017). However, in the absence of a significant interaction in this region between groups, this is merely speculative.

The middle cingulate gyrus was found to be associated with increasing negativity of discrepancy. The midcingulate cortex generally has an established relationship with the experience of pain, and in mediating the affective-motivational component of pain (Vogt, 2005). Previous research has linked this to the experience of negative emotion, and identified the region as a key node in the interaction between negative emotion and motor signals (Pereira et al., 2010). With relevance to the current task, a review from Apps, Lockwood and Balsters (2013) proposed that the gyral surface of the midcingulate cortex was engaged when predicting and monitoring the outcomes of social interactions, and in particular, when tracking the extent to which our behaviour enables us to meet goals when interacting with others. Finding this region activated in response to increasingly negatively discrepant feedback might be indicative of the experience of negative emotions in response to this feedback, and perhaps, monitoring this important social outcome.

Right Precentral Gyrus

The right precentral gyrus was found to be deactivated across conditions in the Depressed group relative to Controls, at the whole brain level. The right precentral gyrus forms part of the primary motor cortex, a region chiefly associated with voluntary motor action (Banker & Tadi, 2020) but also in the modulation of reward (Roesch and Olson, 2003). Accordingly, this region has increasingly been associated with mood, showing activation in response to negative emotional stimuli (Pereira et al., 2011; Kolesar, Kornelsen and Smith, 2017). There is evidence that this activation may have a regulatory role; in a diary study of healthy participants, Ismaylova et al. (2018) found that increased activation in the precentral gyri in response to negative emotional stimuli was associated with greater daily reported positive

mood. Moreover, the right precentral gyrus may be sensitive to the self-relevancy of emotion cues, and has been identified as a key node in the interaction between emotion and action processing in the brain (Portugal et al., 2020). Our observation of increased deactivation of this region in Depressed participants relative to Controls might therefore indicate reduced emotional regulation in this group in response to salient social feedback.

Demographic vs Social Feedback

We found that social feedback, relative to demographic feedback, led to greater activation in the right anterior insula (rAI) and amygdala. The role of the amygdala in social and emotional processing is well established, however, it has a diverse array of functions and likely also subserves perceptions of salience, processing of unpredictability and the experience of reward (Adolphs, 2010), all relevant to the current task. The rAI has been broadly associated with social cognition and empathy (Fan et al., 2011), and with inferring others states of mind (Rilling et al., 2008). It also plays a prominent role in the experience of negative feedback (Seerhausen et al., 2016), experiences of social exclusion (Eisenberger et al., 2009) and negative social emotion (Lamm & Singer, 2010), as well as self-relevant processing including self-reflection (Modinos, Ormel and Aleman, 2009) and self-other comparisons (Kedia et al., 2017). Greater activation of these regions in the Social Condition might indicate that the condition was more effective at stimulating social processing, or that receiving discrepant feedback from others is more emotionally salient than ‘calculated’ feedback.

Limitations and Future Directions

One limitation of this task is that participants were not asked to rate how important they felt each of the feedback adjectives was to their self-concept. Leary and Downs (1995) theorized “only when people have staked their connections to others on certain aspects of themselves should their self-esteem be affected by events that reflect on those aspects”. Accordingly, Schie

et al's (2018) feedback study had participants rate how applicable they felt the feedback was to themselves, and found that regions such as the TPJ, insula and mPFC were differentially activated depending on perceived applicability.

A further potential limitation is that we did not have enough trials to investigate changes in neural responses over time. Eisenberger's' (2004) characterisation of the dACC as a neural alarm system considered that while triggering a change in our attention is useful, for example when dealing with a threat, consistent "full volume" alarm systems may detract from our ability to process and respond to such stimuli. Accordingly, over time, feedback mechanisms (potentially in the right ventral prefrontal cortex; Kawamoto, 2012) might adaptatively down-regulate these signals from the dACC. Such effects have been observed in as few as two feedback sessions (Dedovic, 2016), and might realistically have been observed in our study, in which Controls performed the Social and Demographic Feedback conditions sequentially.

Finally, several of the study's findings had possible implications for emotion regulation; these relationships could have been validated by having participants make ratings of their affect after receiving feedback, a methodology which has been widely used in previous literature. Similarly, we could have controlled for this by providing participants with specific instructions regarding whether to regulate their emotions or not, or asked them after the task whether they felt they had been regulating their emotions (for example, because they were in an unfamiliar place).

Further investigation into a neural signature for the sociometer might be justified in exploring the role of mentalizing regions; Kawamichi et al. (2018) presented participants with reputation feedback, and had participants rate their state self-esteem and the pleasantness of the feedback. They calculated sensitivity to feedback as the rate of change in state self-esteem per unit of pleasantness. They found that sensitivity to feedback was positively correlated with precuneus

activity during feedback trials. Positive feedback was associated with the middle insula, occipital cortex and orbitofrontal cortex, while negative feedback was associated with the dACC, AI, TPJ and superior temporal sulcus. Significantly, functional connectivity of the precuneus with these negative feedback areas was predictive of higher levels of sensitivity. These findings indicate that the sociometer perhaps involves a more complex network which includes mentalizing regions, allowing for the integration of contextual information in modulating the sensitivity of the sociometer.

Conclusions

The work in this thesis aims to expand our understanding of the role of regions of the physical pain network in social function within a socio-evolutionary framework. In this chapter, we investigated whether these regions might constitute a sociometer, and whether individuals with depression exhibit differences in neural activation in response to rank-discrepant feedback. We did not find evidence for our prediction of increased activation in the dACC-AI in depression. Instead, we found evidence of altered activity in several regions associated with emotional control and self-salience; the anterior and posterior insula were deactivated in Depressed participants during positive discrepancies, and deactivated in Controls across discrepancy types, potentially indicating valenced differences in attributions of self-salience in thesegroups. We found that Depressed participants showed bidirectional deactivation in the dACC, as opposed to deactivation in positive discrepancies only in Controls, potentially indicating poorer emotional control. Together, these findings indicate that regions involved in emotionalcontrol and attributions of self-salience are differentially activated in Depressed participants and Controls in response to unexpected social feedback. In a socio-evolutionary context, we might interpret this as evidence that mechanisms involved in positive self-biases and the preservation of self-esteem (commonly observed in Control samples), are influenced by socialfeedback, and may be altered in individuals who perceive themselves as low in social rank.

CHAPTER 6. SENSITIVITY TO FAIRNESS AND SOCIAL NORMS IN AN ULTIMATUM GAME

6.1. INTRODUCTION

The Social Risk Hypothesis of Depressed Mood (SRH) (Allen and Badcock, 2003) posits that depressed mood evolved to minimise the risk of social exclusion in situations where one's status within the group is critically low. Social status, in this context, can best be conceptualised as the ratio between one's social value and social burden to the group, which Allen and Badcock termed Social Investment Potential (SIP). Chapter 1 reviewed evidence that many of the features of depressed mood can be understood in this context – when SIP becomes criticallylow (burden outweighs value), including sensitivity to signals of social threat, and inhibition of risky social behaviours in favour of submissiveness. These features become clinically relevant when the adaptive behaviour is unsuccessful, and SIP remains chronically low, resulting in a 'dysregulated state' detrimental to the individual's long-term wellbeing, such as Major Depressive Disorder (MDD). The purpose of the current study was to investigate the hypotheses of the SRH on social risk in the context of the Ultimatum Game, a well-established neuroeconomic task.

The Ultimatum Game (UG) was devised by Guth et al. (1982), to experimentally investigate a specific form of bargaining behaviour, so-called ultimatum bargaining, in which the set of outcomes is limited to two, and only one participant makes a decision at each stage (Figure 6.1). Although many modifications have arisen since, in the original version, participants are randomly assigned as either Proposer or Responder. The Proposer is asked to divide a stake between the two players; if the Responder accepts the division, then the stake is allocated as suggested, but if they reject the division, both players receive nothing. Traditional models of economic theory assume humans are rational maximisers, that is, they predict that Proposers will offer little to nothing, and Responders will accept any offer over zero (Rubinstein, 1982). Typically, however, Proposers will offer between 30-50% of their stake, and Responders will

reject offers below 30% (Camerer & Fehr, 2004). These findings are consistent in both 'one-shot' and iterated versions of the game (Guth et al., 1982), and have informed many theories of human reciprocity and altruism. The literature therefore generally defines offers of 40% and under as unfair (Wu et al., 2011).

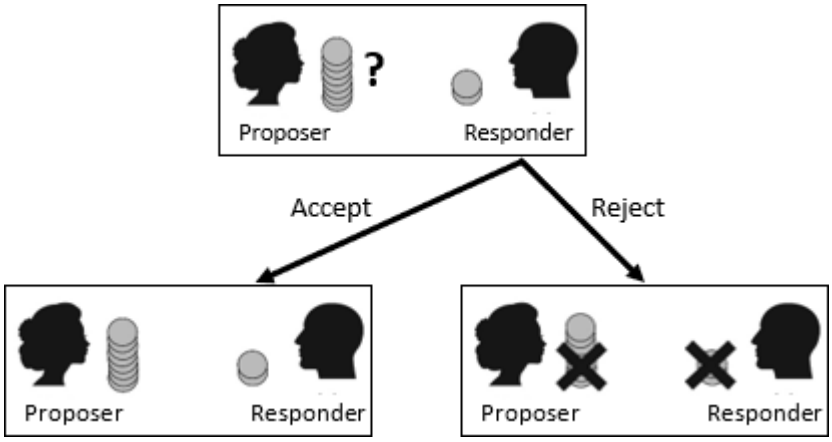


Figure 6.1. Adapted from Pisor et al., 2020. The Ultimatum Game. The Proposer offers a split of their endowment, but each only keeps their share if the Responder accepts.

Some theories which seek to explain the generosity typically observed in the UG claim that generous offers are a consequence of the self-interested desire to encourage high offers from others (Everett, Faber & Crockett, 2015). To reduce this possibility, the current task used a one-shot protocol in which participants made offers simultaneously on the first day of testing (Proposer role) to an experimental 'In-Group' and anonymous 'Out-Group', and returned to see the offers they had received during a functional MRI (fMRI) scanning session on day two (Responder Role). They were informed that there would be no further iterations of the game.

Behavioural Studies of the UG in Depression

Neuroeconomic games mimic real-life, dynamic social interactions within a laboratory setting, providing a valuable ecological paradigm for operationalising and assessing complex social

behaviours (Robson, 2020). Chapter 1 discussed the value of such paradigms for assessing socio-evolutionary theories of affect. Amongst these, the UG may be particularly appropriate for use in our current sample, as depressed groups have shown normative understanding of fairness in the UG, accepting more fair offers than unfair (Robson, 2020). Moreover, the demands on executive function in this task are relatively low (Guth et al., 1982) and have been shown to bear little relation to performance (Woodcock, 2020). Therefore, the UG allows us to test the predictions of the SRH by examining differences in social decision-making and prosociality between our Depressed and Control groups.

The UG has been used widely with depressed samples. As Responder, depressed participants consistently reject more unfair offers than controls (Scheele et al., 2013). A recent meta-analysis of UG experiments in clinical populations found only one of nine studies that did not replicate this finding (Hinterbuchinger, 2017). Moreover, the rejection rate for unfair offers has been shown to correlate with severity of depressive symptoms (Wang, 2014). The severity of symptoms appears to be an important factor, as a review from Robson (2020) highlights that studies which report little or no difference between groups used either non-clinical or mildly symptomatic samples. Pulcu et al. (2015) suggested that the higher rate of rejection of unfair offers in depression may be due to a tendency to focus on the negative emotions and associations of unfair offers, as opposed to the potential gains. This is supported by findings that individuals with low self-esteem and associated depressive symptoms experience greater distress and anger in response to unfair offers than controls (Paz et al., 2017). The idea that high rates of rejection are driven by negative affect might also explain the findings of Harle and Sanfey (2007), who used a mood-induction to generate sadness in non-depressed participants and found that this resulted in higher rejection rates of unfair offers, comparable to an MDD sample. However, a paper from Radke et al. (2013) found that depressed individuals also rejected more fair (5:5) and hyperfair (8:2) offers when compared to controls, which the

authors interpreted as evidence that higher levels of rejection result from the reduced sensitivity to reward in depression, leading to a general reduction in acceptance of offers, irrespective of fairness.

An alternative to affect-based interpretations of higher rejection-rates for unfair offers in depression are reciprocity-based theories, which propose that rejection of unfair offers is a mechanism for enforcing social norms (Falk & Fischbacher, 2006). This aligns with evolutionary theories, such as the SRH, which propose greater sensitivity to social norms in depression. For someone of low rank, enforcing social norms at a cost to oneself provides value to the group, improving ones SIP (Carpenter & Matthews, 2002), moreover, a group with well-upheld prosocial norms might be arguably less prone to ejecting its members. Harris et al. (2020) hypothesised that cognitive resources were needed to resolve the conflict between economic self-interest and social status, and therefore that in situations where cognitive resources were taxed (in this case by mentally counting tones) players would accept more unfair offers. They found this hypothesis was supported, but only when the Proposer was defined as “High-status”, that is, when participants had fewer cognitive resources available to consider the offer, they preferentially accepted offers from high-status players regardless of monetary ‘fairness’. Additionally, participants who rated themselves as close in social status to the High-status Proposer were more likely to accept unfair offers from them, while participants who felt close in status to low-status Proposers were more likely to reject their unfair offers. Supporting these findings, Yamagashi et al. (2012) suggested rejection of unfair offers is based on concerns about inferiority, in that participants were more likely to accept an inferior status relative to a high-status proposer than to a low-status proposer. These studies can be understood in the context

of the SRH and its predictions regarding depression and social status; if depressed participants perceive themselves to be of low status, a greater proportion of unfair offers would be rejected, as they reject from high-status Proposers due to the large difference in status and reject from low-status Proposers due to the closeness of status.

Overall, behavioural studies of the UG in depressed participants have found a stronger adherence to social norms, demonstrated as reliably rejecting offers that are considered unfair. Few studies have placed depressed participants in the role of Proposer in the UG; however, those that have find this group make higher offers than controls (Scheele et al., 2013; Destoop et al., 2012), demonstrating a sense of prosociality. This is highly relevant in the context the SRH, which proposes greater sensitivity to social norms in low-status individuals, and a need to provide value to the group through prosocial behaviours. The current study aims to extend this work, placing our Depressed sample in the role of Proposer.

Imaging Studies of Fairness

There have been several fMRI studies examining neuroeconomic games of fairness in healthy samples (Sanfey, 2003; Trepel, Fox & Poldrak, 2005; Tabibnia et al., 2008; Guroglu et al., 2010; Baumgartner et al., 2011; Grecucci et al., 2013; Feng, Luo & Krueger, 2015). A fair offer in the UG produces little conflict for the Responder; the offer is usually accepted, and the game continues (Tabibnia and Lieberman, 2007). These offers are associated with relatively greater activation in reward brain regions in the Responder, such as the ventromedial prefrontal cortex (vmPFC), orbitofrontal cortex, ventral striatum and midbrain dopamine regions (Baumgartner et al. 2011; Trepel, Fox & Poldrack, 2005), reinforcing the notion that fairness is a rewarding experience. An unfair offer, however, arguably produces a conflict in the Responder between motivations of economic self-interest and social-norm enforcement, which interact with the negative emotional implications of unfair treatment (Fehr & Camerer, 2007). Imaging of these

offers has therefore contributed to the literature explicating automatic versus controlled processes in social psychology (Lieberman, 2007).

The automatic processes during unfair offers involve the evaluation and socioemotional processing of norm violations. These processes have been associated with relatively enhanced activation in the amygdala (Yu, Calder & Mobbs, 2014), anterior insula (AI) (Guo, et al. 2013) and ventromedial prefrontal cortex (vmPFC) (Xiang et al., 2013). These regions are also associated with greater punishment of social norm violations (Gospic et al. 2011), supporting the idea that they may form an automatic, emotion-based system for enforcing these norms, which needs to be balanced against the consideration of economic factors. This could be achieved either via the downregulation of emotion reactivity, or by increased executive control motivated by economic self-interest, or a combination of the two. Previous work on emotion-regulation implicates the ventrolateral prefrontal cortex (vlPFC) and dorsomedial prefrontal cortex (dmPFC) for the former role (Wager et al., 2008). In a study specific to emotional control in the UG, Grecucci et al. (2013), instructed participants to regulate their emotions and reappraise offers. They found thatincreased use of reappraisal was associated with greater activity in the inferior and middle frontal gyrus, medial PFC and cingulate gyrus, and up or down regulation of emotion was associated with more or less activation in the posterior insula, respectively. Meanwhile, executive control within the context of the UG has been associated with activity in the right dorsolateral PFC (dlPFC); Baumgartner et al. (2011) found that during high-conflict trials, control subjects made more personally costly decisions than a sample who received Transcranial Magnetic Stimulation of the dlPFC. The dorsal anterior cingulate cortex (dACC)has been suggested as a possible region associated with monitoring of this conflict (Fehr & Camerer, 2007).

Feng, Luo and Krueger (2015) consolidated many of these findings in a coordinate-based meta-analysis of fMRI studies of the UG. They found that reported activations converged on two networks, representing a so-called 'intuitive' system for recognizing social norm violations, and a so-called 'deliberate' system for integrating economic self-interest with social status concerns, to generate decisions. The first system is rooted in the anterior insula and vmPFC, while the second system is underpinned by activations across the vlPFC, dmPFC, left and right dorsolateral PFC and rostral ACC. The authors suggest that monitoring of economic self-interest might be associated with activation in the dorsal anterior cingulate cortex (dACC) and describe a mechanism by which conflicts between the intuitive system, reflected in the AI and vmPFC, and economic interests, in the dACC, are resolved by the deliberate system suppressing one or the other motivations. Imaging hypotheses based on this meta-analysis of the UG are that our Depressed group will show increased activity in brain regions associated with social status concerns during unfair offers, primarily in the AI and vmPFC.

As we have seen, one neural region commonly associated with unfairness during the UG is the anterior insula (AI) (Sanfey, 2003). This is likely due to the region's association with the processing of social norms; Xiang, Lohrenz and Montague (2013) performed an UG in which participants were preadapted to either high or low offers using a norm training paradigm, and found that norm-prediction errors correlated with activity in the AI and ventral striatum. AI activation has also been associated with the enforcement of these social norms through punishment; Spitzer et al. (2007) found that the AI showed greater activation when participants had the option to punish each other for unfair decisions (social condition) than in identical trials where the punishment was administered by computer (non-social). Interestingly, reductions in functional connectivity between the anterior insula and other regions associated with inequality such as the orbitofrontal cortex and putamen, has been found to correlate with a higher propensity to spend money in order to increase the payoffs of others (Yu, Calder & Mobbs,

2014). Alongside the social norm function is the possibility that activation in the AI during unfair trials represents a negative emotional response to unfairness, based on previous evidence of its involvement in negative affective states (Uddin et al., 2018). In support of this, Tabibnia et al. (2008) report the results of an UG which found that although AI activation was greater during unfair trials, this activation was lower in unfair trials that were accepted than those that were rejected, and that this decrease inversely correlated with ventrolateral prefrontal cortex (vlPFC) activation. Given the relationship of the vlPFC with emotion regulation (He et al., 2018), the authors suggest that the activation of the AI is indicative of negative affective responses to offers, which subsequently drive acceptance or rejection of the offer.

The involvement of the AI might therefore be interpreted in association with both a negative emotional reaction to unfairness, and error signalling in response to norm violations. These functions are not necessarily discrete, and the overlap has prompted some authors to suggest that emotions might be underwritten by their own error signals, used to "direct the organism to zero", that is, to motivate us towards a homeostatic state (Montague &Lohrenz, 2007).

Imaging Fairness Depression

Gradin et al. (2015) performed the only previous fMRI study of the UG with a depressed group. They found that increasing unfairness of offers was associated with increasing activation in the dACC and insula in both depressed and control samples acting as responders. The dACC and the anterior region of the insula have previously been associated with positive and negative social evaluations (e.g., Dalgleish et al., 2017) as well as social pain (Eisenberger, Lieberman & Williams, 2003), conflict monitoring (Botvinick et al., 2001) and expectancy violation (Arulpragasm et al., 2018). In non-depressed controls, increasing fairness of offers was associated with greater activation in the nucleus accumbens and dorsal caudate, regions typically implicated in the processing of reward.

Gradin et al. (2016) also performed a study using another neuroeconomic game – the Prisoner's Dilemma – with a depressed sample. In this game, players choose independently whether they would like to cooperate or defect during a cooperative task where a given amount of money is at stake. If both players choose to cooperate then they receive an equal share of the money, if they both choose to defect then neither receives anything, and if only one chooses to cooperate and the other chooses to defect, the defector receives the whole sum. Activation was compared between 'balanced' trials, in which both participants chose the same action, and 'imbalanced' trials, in which participants chose differing actions. In imbalanced trials, both control and depressed samples showed increased activation in the AI and dorsolateral prefrontal cortex (dlPFC). However, depressed samples showed significantly less left dlPFC activation than controls, with the reduction correlating with self-reported feelings of guilt. The dlPFC has been associated with emotion regulation (Golkar, 2012) and the authors concluded that this suggested that this reduced activation reflected greater feelings of unregulated negative affect in the depressed group.

The Role of In- and Out-Groups

Preferential treatment for in-group members is a well-documented human bias (Pavey et al., 2011; Fehr et al., 2008). Theoretical explanations for this behaviour can be spilt into preference-based accounts, which explain in-group treatment as the result of an evolved and intuitive prosociality (Fehr and Schmidt, 1999), and belief-based accounts, which rely more on expectations and strategy (Blanco et al., 2014). Core to much of this work is the idea of reciprocity; reciprocity is explained by belief-based accounts as a strategic decision, intended to improve one's reputation and invoke future prosocial behaviours from others, whereas preference-based accounts view reciprocity as simply reflective of our preference to behave pro-socially towards those who have been prosocial to us, and thus weight the intentions of others more highly than financial or strategic outcomes (Everett, Faber & Crockett, 2015). These are sometimes termed 'weak' and 'strong' reciprocity, respectively (Falk & Fischbacher, 2006).

Attempts to characterise such group preferences in the UG have produced mixed results. McLeish and Oxoby (2011) investigated the role of group membership by priming participants that they were playing with either an in- or out-group co-player. They found that participants offered more to in-group players, but also reported higher minimum acceptable offers from them, indicating stronger enforcement of prosocial norms within groups. This aligns with findings from a gift-giving paradigm by Shinada, Yamagishi and Ohmura (2004), which found that non-cooperative in-group players were punished more harshly than similarly non-cooperative out-group players.

Conversely, Valenzuela and Srivastava (2012) found that participants were more likely to accept unfair offers from in-group members (students at the same university) than out-group members (a competing university). Similarly, Brune et al. (2012) used a hypnotic induction to

instil group membership and found greater acceptance of unfair offers when they were made by the in-group. These findings would seem to align with preference-based accounts, whereby in-group members are treated more altruistically, and this is supported by studies which find in-group members are less likely to be punished for misbehaviour than out-group members (Chen & Li, 2009).

There is little imaging work relating specifically to group preferences during the UG. Considering group preferences more broadly identifies many of the same brain regions associated previously with social norms; Hein et al. (2010) used a protocol in which participants could choose to endure physical pain in order to reduce the pain of an in-group or out-group member. Helping an in-group member was predicted by activation of the AI, while lack of helping an out-group member was associated with activity in the nucleus accumbens. Observation of pain in in-group members is consistently associated with more activation, relative to observing out-group members, in regions related to empathy and pain, such as the AI (Contreras-Huerta et al., 2013) and dACC (Xu et al., 2009). Watching in-group members in pain or during conflict is also associated with more activity in mentalizing regions including the tempoparietal junction (TPJ) and mPFC (Cheon et al., 2011). These studies demonstrate differences in regions associated with empathy and mentalizing when interacting with in- and out-group members.

According to belief-based accounts, cooperation and reciprocal behaviours are the result of a desire to avoid being viewed violating social norms (Fehr and Fischbacher, 2004) and to build one's reputation (Milinski et al., 2002). In line with the Social Risk Hypothesis of Depressed Mood (see Chapter 1) these should be chief concerns for individuals with depression and should be particularly salient with regards to the in-group, which informs the hypotheses for the current task. The Ultimatum Game provides a quantifiable method for assessing these interpersonal behaviours; The Proposer decides how much of their sum they would like to offer

the Responder, and the Responder can then choose to accept or reject the offer, with rejection resulting in neither player receiving a pay out.

Hypotheses

Based on the predictions of the Social Risk Hypothesis (Allen & Badcock, 2003), for the behavioural data we predicted that Depressed group members acting as Proposers would make higher offers than Control group members overall, and when making offers specifically to the In-Group. We predicted that, across groups, size of offers to the In-Group would correlate with severity of depressive symptoms and submissive behaviours. As responders, we predicted that the Depressed group would exhibit greater enforcement of social norms, by rejecting more unfair offers, defined as offers of 4 and under, than the Control group, and that this tendency would be strongest when responding to the in-group than the out-group.

In terms of imaging data, we predicted that the Depressed group would show greater sensitivity to offer value in the AI and vmPFC than Controls – regions previously proposed as the basis of an intuitive system for the recognition of social-norm violations – as well as greater activation in regions associated with social pain such as the dACC.

6.2. METHODS

Participants

Full participant demographics, recruitment procedures and exclusion criteria are detailed in Chapter 3. In the current task, 5 participants were excluded from the Depressed group due to expressing disbelief in the protocol (n=3) or failures in data acquisition (n=2). Participants were therefore 57 adults (35 female, range 18-64, mean=45.65yrs) recruited from the MRC CBU volunteer panel. This comprised 32 Control participants (20 female, age range 18-64, mean=44.85yrs) and 25 Depressed participants (15 female, age range 21-64, mean=48.33yrs).

There were no significant differences between the groups in relation to gender ($X^2(1, N=58)=.050$, $p=.822$) or age ($t(56)=-1.50$, $p=.139$). The Depressed group had an average Beck Depression Inventory-II score of 25.45 (falling within the moderate range, 20-28), which was significantly different to the Control average of 5.45 ($t(56)=-8.32$, $p=<.001$).

Protocol

The task was part of a larger protocol, carried out over two days (see Chapter 3 for details). On the first day, participants completed two behavioural tasks with a group of four other participants, to establish an "In-Group" (these tasks are detailed in Chapters 7 and 8). Following these tasks, participants completed the "Offers" stage of the UG, discussed here. On the second day, participants returned to complete a functional Magnetic Resonance Imaging (fMRI) session. This session included the "Accept/Reject" stage of the UG, discussed here.

Group Testing Session on Day One

On Day One, participants played the role of Proposer. Participants were given an information and response sheet, which explained the premise of the UG and collected their offers (Appendix 6.1). The sheet had two sections, with the order counterbalanced across participants. One section of the sheet represented the In-Group condition; participants were told they were playing the game with each of their fellow group members in turn and entered the offers they wanted to make on the sheet. Participants made 6 offers to each of their 4 fellow participants, with varying endowment sizes up to £5 (Larney, Rotella & Barclay, 2019), creating 24 Proposer offers per participant. They were informed that their fellow participants would see these offers the next day during the imaging session and would have the chance to accept or reject them. The other section of the sheet represented the Out-Group condition; participants were told that they were playing against anonymous subjects from another testing group. Offers

were made in the same way and across the same stakes as the In-Group condition. This sheet was read aloud by the experimenter and participants had the opportunity to ask questions.

Questionnaires

As part of the larger protocol, participants completed questionnaires related to mood and social processing (full details in Chapter 3). To reduce the number of tests, not all questionnaires were included in every analysis. Four were included in the analysis of the current task; The Beck Depression Inventory-II (BDI-II; Beck, Steer & Brown, 1996) was included as a measure of affect, while the Submissive Behaviour Scale (SBS; Allen & Gilbert, 1997) Striving to Avoid Inferiority Scale (SAIS; Gilbert, Broomhead, Irons & McEwan, 2007) and Involuntary Subordination Questionnaire (ISQ; Sturman, 2011) were included as measures of social function.

Imaging Session

The protocol of the scanning session was taken from Gradin et al. (2015). During the session participants played the role of Responder, viewing offers in the scanner and choosing to accept or reject them using a button box. The protocol began with a 20-second information screen which reminded participants of the rules of the UG, informed them of how the imaging task would proceed and instructed use of the button box. Participants saw 48 offers in total, 24 from their groupmates, the In-Group condition, and 24 from unknown participants in different testing groups, the Out-Group condition. The offers were fixed by the experimenter to ensure an equal split of unfair (<4) and fair (4-6) trials across conditions. Each offer epoch comprisedthree components and a fixation slide (Figure 6.2). First was a 2-second Group Identifier Slide,which informed participants of the identity of the Proposer, either “Your Group” (In-Group trials) or “Other” (Out-Group trials). Then a 3-second Offer Slide in which participants saw how many tokens they had been offered out of 10. The third slide was the response screen

which read "Accept the Offer?", to which participants could respond Yes or No. This slide was untimed, although participants were encouraged to choose their initial response. Finally, the fixation slide was presented, which was jittered between 1-4 seconds before the next epoch. Participants completed a believability questionnaire (Appendix 5.3) after scanning and were fully debriefed on the manipulation.

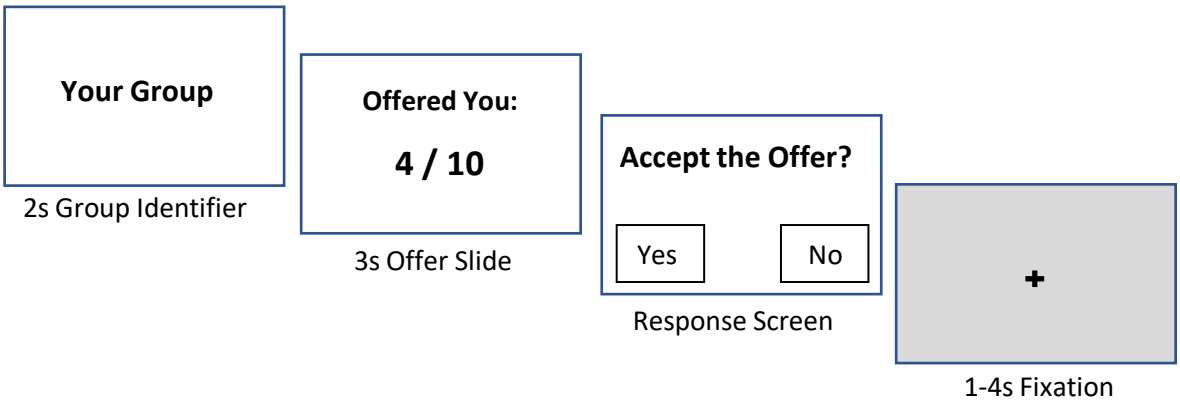


Figure 6.2. Slides and timings sequence for one offer epoch as it appeared to participants in the scanner. Each run contained 48 offers, 24 In-Group and 24 Out-Group.

Data Analysis

Behavioural Data

For each participant, the average percentage of their tokens that they offered in the role of Proposer on Day One was calculated, separately for the 24 offers they made to the In-Group (InGroupOffer) and the 24 they made to the Out-Group (OutGroupOffer). A mean across groups was also computed resulting in three variables, BothGroupsOffer, InGroupOffer and OutGroupOffer. To test our main hypotheses, a two-way ANOVA was performed, with Clinical Group and Responder Group as independent variables and the mean percentage offer as the dependent variable. Interpreting the results of this ANOVA, follow-up independent samples t-tests were run between Depressed and Control participants, and paired samples t-

tests were run between the InGroupOffer and OutGroupOffer variables, both across and within clinical groups. To test our hypothesis that In-Group offers would be correlated with depressive symptoms and submissive behaviours, Pearson correlations were run between the four selected questionnaire measures and the InGroupOffer and OutGroupOffer variables.

In terms of the behavioural data when participants were acting as Responders in the fMRI session on Day Two, a repeated measures ANOVA was performed to investigate the effects of Clinical Group (Depressed versus Control as Responder) and Proposer Group (In-Group or Out-Group member) on whether an offer was accepted or not. Finally, we investigated whether the relative submissiveness of the Responder in a given In-Group trial effected the value of the offer made by the Proposer; a variable was generated which represented the difference in submissiveness between the two players, termed SBSDifferenceScore. This was the Submissive Behaviour Scale (SBS) score of the Proposer minus the SBS score of the Responder. High scores were therefore indicative of the Proposer being relatively more submissive. Pearson Correlations were run between this variable and the InGroupOffer variable.

Imaging Data

Details of image pre-processing are reported in Chapter 3. We corrected for multiple comparisons using a cluster-wise Family-wise error (FWE) threshold of 0.05, using an initial cluster-defining height threshold of $p<0.001$ uncorrected with a *k* cluster extent threshold of 194 voxels (https://zenodo.org/record/1689891#.YUrhE33TU2w). We investigated three factors; Fairness, Proposer Group, and Decision. Each of these was examined in a two-level analysis using SPM12. For Fairness, at the first level, a linear GLM was applied to the time series within each voxel. The BOLD response was modelled by convolving a canonical hemodynamic response function (HRF) to each fairness type (Fair and Unfair). In line with previous literature,

offers of 4 and under (out of 10) were defined as unfair (Wu et al., 2011). Contrasts were generated for Fair Offers (Fair minus Unfair) and Unfair Offers (Unfair minus Fair). These contrasts were taken to the second-level and entered into an ANOVA with Clinical Group (2 levels: Depressed, Controls) and Fairness (2 levels: Fair Offers, Unfair Offers) as the conditions of interest.. A follow-up analysis was performed to investigate whether any regions were associated with increasing or decreasing fairness, in which all trials were combined into a single condition and the offer value was introduced as a parametric modulator, as a proxy for fairness.

The effect of In-Group and Out-Group membership was investigated similarly by modelling BOLD responses to In-Group and Out-Group offers separately at the first-level, generating contrasts for each Proposer type, and running these contrasts at the second-level in a two-way ANOVA with factors of Clinical Group (2 levels: Depressed, Controls) and Proposer Group (2 levels: In-Group, Out-Group). Decision type was investigated with a third ANOVA, with two factors of Clinical Group (2 levels: Depressed, Controls) and Decision (2 levels: accepted, rejected). An exploratory second level analysis was run using scores on the Submissive Behaviour Scale (SBS), Involuntary Subordination Questionnaire (ISQ) and Striving to Avoid Inferiority insecure subscale (SAIS-I) as covariates against the contrasts in each ANOVA.

Finally, each of the contrasts generated in the three ANOVAs and the Parametric Analysis were run against six predetermined ROIs using MarsBar in SPM12. ROIs were the dACC and AI regions, as identified by Dalgleish et al. (2017) (dACC peak voxel x=2, y=32, z=24, left AI peak voxel x=-28, y=18, z=-10), as well as four regions of the mentalizing network. A search for “Mentalizing” on Neurosynth (www.neurosynth.org) produced 124 studies. Peak voxel co-ordinates for the dmPFC, vmPFC, Left TPJ and Precuneus were all taken from this map and used to produce 10mm spheres which formed the ROIs (centre coordinates for dmPFC x=4/y=52/z=24; vmPFC x=-2/y=48/z=-18; Left TPJ x=-48/y=-56/z=22; Precuneus x=2/y=-54/z=40).

6.3. RESULTS

Behavioural Analyses

A within-groups outlier analysis was run on offers made by participants in the role of Proposer; Z values were calculated and values +/-3 were excluded from analysis (Seo, 2006), resulting in the removal of 37 of 1326 data points (Table 6.1).

PPID	Percentage of Tokens	Z Value
Controls		
110723	100 (4 trials)	4.06165
110725	100 (2 trials)	4.06165
280343	100	4.06165
210323	90	3.30501
Depressed		
040723	100 (5 trials)	4.06165
230551	90 (12 trials)	3.30501
	95 (4 trials)	3.68333
110414	100	4.06165
160421	100	4.06165
160424	100 (4 trials)	4.06165

Table 6.1. Outlier trials removed. 37 of 1326 trials were removed, 2.7% of the dataset

After the removal of these outliers, the mean percentage of the tokens that each participant offered was calculated (TotalOffer) and then separately for In- (InGroupOffer) and Out-Group (OutGroupOffer) conditions. There was no significant difference between genders in either the In-Group or Out-Group conditions (In-; $t(55)=.48$, $p=.63$, Out-; $t(55)=.88$, $p=.38$), nor was there any significant correlation with age (In; $r(55)=.16$, $p=.255$, Out; $r(55)=.16$, $p=.243$).

Main Predictions: Offers

A two-way ANOVA was run with Clinical Group and Responder Group as independent variables and the mean percentage offer as the dependent variable. This analysis found no significant interaction between the variables ($F(1,112)=.74$, $p=.393$), however, there was a main effect of Clinical Group ($F(1,112)=5.87$, $p=.017$). A follow-up independent samples t-test was run on the TotalOffer variable, which confirmed a significant difference in the offers made by the Depressed ($M=.47$, $SD=.06$) and Control ($M=.42$, $SD=.08$) groups ($t(55)=2.84$, $p=.006$), with the Depressed participants making higher offers as predicted.

Further independent samples t-tests were then run for the InGroupOffer and OutGroupOffer variables. Concerning the In-Group, there was a significant difference in the offers made by Depressed ($M=.48$, $SD=.08$) and Control ($M=.42$, $SD=.07$) participants ($t(55)=-2.73$, $p=.008$, $d=.725$), with the Depressed group making higher offers. Concerning the Out-Group, no significant difference was found between Depressed ($M=.48$, $SD=.06$) and Control ($M=.46$, $SD=.12$) groups ($t(55)=-.97$, $p=.337$) (Figure 6.3).

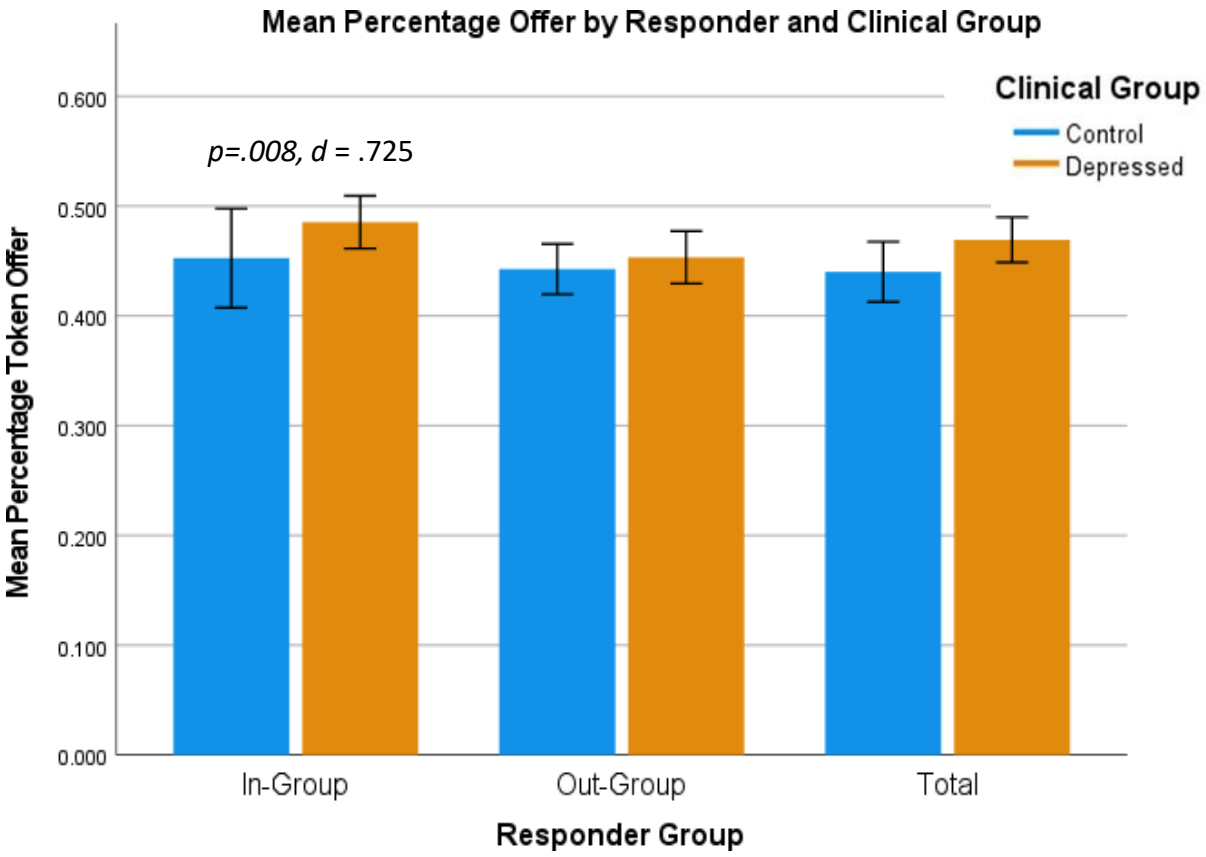


Figure 6.3. Overall, the Depressed Group made significantly higher offers than Controls p = .006, d =.644. There was a significant difference between Depressed and Control Groups Offers to the In-Group, p=.008, d=.725. There was no significant difference in offers to the Out-Group, p=.337.

A paired samples t-test run across both Depressed and Control participants found a significant difference between offers to the In-Group (M=.47, SD=.10) and Out-Group (M=.44, SD=.07) (t(55)=-2.47, p=.017). When Depressed and Control participants were analysed separately the significance did not survive (Depressed; t(24)=-2.06, p=.051, Controls; t(31)=-1.80, p=.082).

Main Predictions: Decision

A repeated measures ANOVA was run to investigate whether Depressed and Control Groups, as Respondents, differed in the Offers they accepted based on the Fairness of the Offer and the group membership of the Proposer. Within-subjects factors were Fairness (Fair>4/Unfair<4)

and Proposer Group (In-Group/Out-Group), the between-subjects factor was Clinical Group with 2 levels (Depressed and Controls), and the dependent variable was the rejection rate, i.e. what proportion of offers of that value were rejected.

The results indicated that Fairness had a significant impact on rejection rate, as would be expected ($F(1, 55)=146.08$, $p<.001$, $n_p^2=.726$), in that lower offers were rejected more than higher offers (Figure 6.4). There was a significant effect of Proposer Group, indicating that rejection rates differed depending on whether the Proposer was a member of the In-Group or the Out-Group ($F(1, 55) = 8.89$, $p=.004$, $n_p^2=.139$) with a higher rejection rate for Out-Group offers (44.7% rejection vs 39.2%) (Figure 6.4). Failing to support to our predictions there was no significant interaction between Fairness and Clinical Group ($F(1, 55)=1.28$, $p=.264$, $n_p^2=.023$), or Proposer and Clinical Group ($F(1,55)=1.68$, $p=.201$, $n_p^2=.030$).

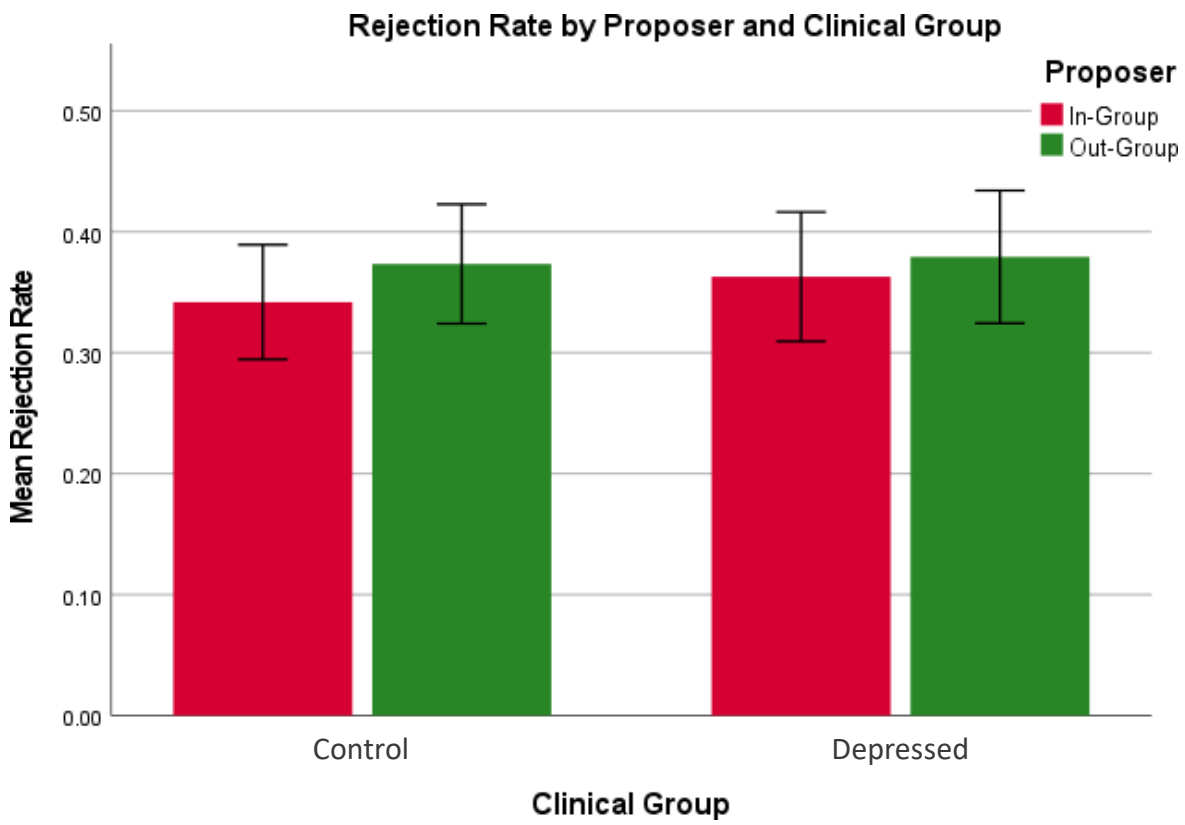


Figure 6.4. Both Groups rejected Out-Group offers more frequently than In-Group offers

Previous literature has indicated that increased rejection of unfair offers may only be present in samples with moderate and severe depressive symptoms (Robson, 2020). Therefore, the repeated measures ANOVA was rerun including only Depressed participants scoring above 18 on the BDI (bringing the total participants in the Depressed group to 22). This analysis found a significant interaction between Fairness and Clinical Group ($F(1, 53) = 5.66$, $p=.021$, $n_p^2=.098$) indicating that Depressed participants with moderate-severe symptoms rejected more unfair offers and less fair offers than Controls (Figure 6.5).

Figure 6.5. Depressed group participants with moderate-severe symptoms rejected unfair offers at a higher rate than Control group participants

Two additional repeated measures ANOVAs were run utilising Offer Value (1-10) as a continuous Fairness metric (see Appendix 6.2). The binary Fairness metric (Fair/Unfair) is

presented here to correspond with the following neuroimaging analysis, which also utilised a Fair/Unfair comparison.

Covariates

We predicted that higher levels of depressive symptoms and submissive behaviour would correlate with making higher offers to the In-Group. We found that the data supported this prediction; Across Groups, positive correlations were found between Offers to the In-Group and scores on the BDI, ISQ and SBS (BDI; r(57)=.37, p=.004, ISQ; r(57)=.29, p=.023, SBS; r(57)=.42, p=.001) and a negative correlation was found with the secure subscale of the SAIS (r(57)=-.39, p=.002) (Table 6.2). No correlations were found with Out-Group offers. A Fischers Z transformation was used to compare covariate correlations with In-Group and Out-Group Offers (Eid, Gollwitzer & Schmidt, 2011), finding a significant difference for the SBS (Z=1.73, p=.042), SAIS-S (Z=2.52, p=.006) and BDI (Z=1.95, p=.026), indicating that these measures correlated significantly better with In-Group than Out-Group offers.

Responder	Measure	R	df	p
Across Clinical Group				
In-Group	Beck Depression Inventory	.37	58	.004
	Involuntary Subordination Questionnaire	.29	58	.023
	Submissive Behaviour Scale	.42	58	.001
	Striving to Avoid Inferiority – Secure	-.39	58	.002

Table 6.2. Offers to the In-Group were associated across groups with depressive symptoms and submissive behaviour.

Relative Submissiveness

A whole sample Pearson correlation test found a significant correlation between InGroupOffer and SBSDifferenceScore (R(1308)=.08, p=.006). Within-group Pearson correlation tests found

that this correlation was non-significant in the Control group (R(720)=-.02, p=.620); however, in the Depressed group, there was a strong correlation (R(600)=.17, p=.000), indicating that the more submissive the Proposer was relative to the Responder, the more they offered. Fischers Z transformation found a significant difference between the correlations in the two groups (Z=2.83, p=.002).

Imaging Analyses

Exploratory Whole Brain Analyses

The Fairness ANOVA found a significant main effect of Clinical Group, with greater activation in the bilateral occipital pole, superior parietal lobule and superior frontal gyrus in the Depressed Group relative to Controls (Table 6.3). There was a similar main effect of Clinical Group in the Accepted/Rejected ANOVA, revealing greater activation in the bilateral occipital pole, superior parietal lobule and superior frontal gyrus in the Depressed group relative to Controls (Table 6.4). There was also a similar main effect of Clinical Group for the InGroup/Outgroup ANOVA, again revealing greater activation in the bilateral occipital pole, superior parietal lobule and superior frontal gyrus in the Depressed group relative to Controls (Table 6.5). Contrast estimates for activation in the Superior Frontal Gyrus across the effects of interest are shown in Figure 6.6. No significant deactivations were observed, and no significant results were found at the FWE level as a function of offer value.

Region	k	Z value	*Cluster-Level P*	MNI coordinates		
				x	*y*	*z*
Main Effect of Group						
Bilateral occipital pole, bilateral cuneus, bilateral lingual gyrus	5171	7.10	0.000	4	-94	2
Superior Parietal Lobule	701	4.68	0.000	24	-62	62
Superior Frontal Gyrus, Anterior Cingulate Cortex	626	4.91	0.000	-10	40	22

Table 6.3. The Fairness ANOVA found a significant effect of Clinical Group

Region	k	Z value	*Cluster-Level p*	MNI coordinates		
				x	*y*	*z*
Main Effect of Group						
Bilateral occipital pole, bilateral cuneus, bilateral lingual gyrus	4171	6.43	0.000	0	-90	-4
Superior Parietal Lobule	347	4.23	0.002	26	-62	62
Superior Frontal Gyrus, Anterior Cingulate Cortex	697	4.74	0.000	-10	28	44

Table 6.4. The Accepted/Rejected ANOVA found a significant effect of Clinical Group

Region	k	Z value	*Cluster-Level p*	MNI coordinates		
				x	*y*	*z*
Main Effect of Group						
Bilateral occipital pole, bilateral cuneus, bilateral lingual gyrus	5007	6.39	0.000	4	-94	2
Superior Parietal Lobule, Precuneus	551	4.44	0.000	4	-64	58
Superior Frontal Gyrus, Anterior Cingulate Cortex	842	5.15	0.000	-10	40	22

Table 6.5. The InGroup/OutGroup ANOVA found a significant main effect of Clinical Group

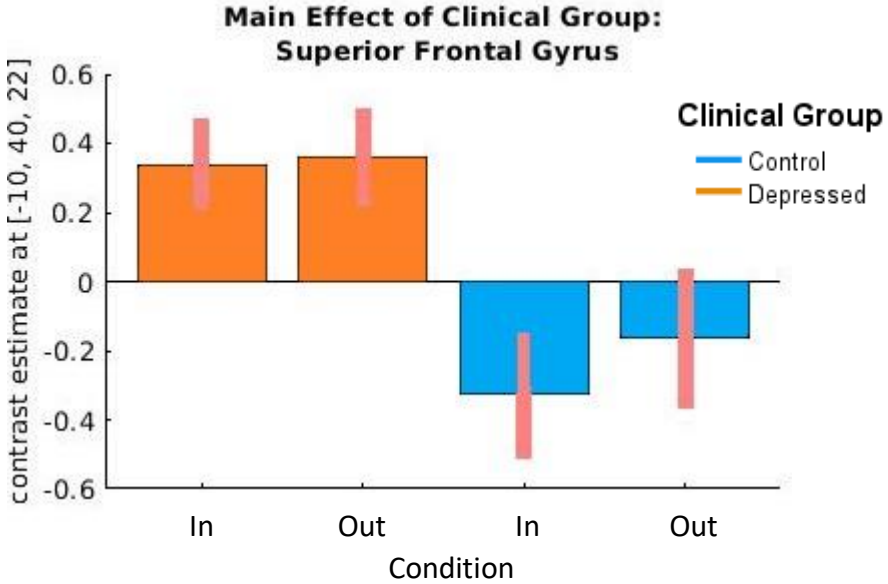


Figure 6.6. Contrast Estimates for the Main Effect of Clinical Group in the In-Group/Out-Group ANOVA, showing greater activation in Superior Frontal Gyrus in the Depressed group across both In-Group and Out-Group conditions

Region of Interest Analyses

ROI analysis of the Fairness ANOVA contrasts did not find any significant regions for Main Effect of Clinical Group, Main Effect of OfferType (Fair/UnFair) or Interaction between Clinical Group and OfferType (Appendix 6.3).

ROI analysis of the Accepted/Rejected ANOVA contrasts did not find any significant regions for Main Effect of Clinical Group, Main Effect of Decision (Accepted/Rejected) or Interaction between Clinical Group and OfferType (Appendix 6.4).

ROI analyses of the InGroup/OutGroup ANOVA contrasts found a significant Main effect of Clinical Group in the dmPFC (Table 6.6). Follow-up analyses found greater activation in the dmPFC in the Depressed Group relative to Controls both across conditions, and within the InGroup contrast (Table 6.6). No significant regions were found for the Main Effect of

Proposer (InGroup/OutGroup) or Interaction between Clinical Group and Proposer (Appendix 6.5).

	Extra SS	F statistic	Corrected p
Main Effect of Clinical Group			
dmPFC	3.50	7.01	0.047726*

	Contrast Value	T Statistic	Corrected p
Depressed (In & Out)>Control(In & Out)			
dmPFC	0.84	2.65	0.029220*
Depressed InGroup > Control InGroup			
dmPFC	0.53	2.40	0.045562*
Depressed OutGroup> Control OutGroup			
dmPFC	0.32	1.37	0.422049

Table 6.6. ROI analyses found greater dmPFC activation in the Depressed group relative to Controls. * indicates significance to the corrected p level

Whole brain exploratory analysis of the covariates did not produce any activations at the FWE level.

6.4. DISCUSSION

The Social Risk Hypothesis of Depressed Mood (SRH; Allen & Badcock, 2003) posits that depressed mood is an adaptive response to low Social Investment Potential, in which individuals reduce their risk of exclusion from their social group by engaging in fewer high-risk social behaviours. The current study tested this hypothesis in the context of the Ultimatum Game (UG), predicting that Depressed participants would show stronger adherence to social norms of reciprocity. We found that our main predictions were supported, as Depressed participants made significantly higher offers than Controls, and offers to the In-Group correlated with measures of depressive symptoms and submissive behaviour significantly more than offers to the Out-Group. Consistent with previous research, participants with moderate-

severe symptoms (BDI>18) rejected more unfair offers than Controls, which has been interpreted as altruistic enforcement of social fairness norms.

Regarding the neuroimaging data, we predicted that the Depressed group would show greater brain activation in response to unfair offers in the AI and vmPFC, which have been previously proposed as regions implicated in an intuitive system for the processing of social-norm violations and social status concerns (Feng, Luo & Krueger, 2015), as well as greater activation in mentalising regions and regions associated with social conflict monitoring (Xiang, Lohrenz & Montague, 2013). We did not find this prediction supported in either the whole-brain or region of interest analyses, instead, the Depressed group exhibited greater activation in three broad regions; the bilateral occipital pole, superior parietal lobule and superior frontal gyrus. These findings were robust across three analyses of the data. Of these, the observed activation of the superior frontal gyrus and anterior cingulate cortex (ACC) may be the most relevant in the current context, given that the ACC has been previously associated with social conflict monitoring and concerns about economic self-interest in the UG (Fehr & Camerer, 2007). Our findings might therefore indicated heightened sensitivity to the social fairness context of the task. Additionally, ROI analyses found the dmPFC was significantly more activated in Depressed than Control participants during InGroup offers; previous research has proposed the dmPFC as a deliberative region which integrates concerns about social status with economic interests in the UG (Guroglu et al. (2010), perhaps indicating greater deliberation by the Depressed group in this socially salient context.

Depression and the Social Risk Hypothesis

In interpreting our findings and their relevance to the Social Risk Hypothesis (SRH) it is useful to reiterate that the SRH does *not* specifically predict increases in either altruism or prosocial behaviours in depression. Rather, it hypothesises that depressed mood can help preserve social

relationships and avoid exclusion, from which we can predict that individuals with depression are able to improve their social value and avoid social risks more effectively and inhibit appetitive drives more adaptively (Allen & Badcock, 2003).

We found that the Depressed group made higher offers than Controls on the UG, both when the In-Group and Out-Group conditions were grouped together, and when the In-Group condition was considered individually. Offers to the In-Group were correlated positively with scores on the BDI, SBS and ISQ, additionally, offer size correlated with the relative SBS score of the Responder, significantly more in the Depressed group than Controls. Relatively few studies have examined depressed samples in the role of proposer, however, our findings are in line with those that have (Scheele et al., 2013; Destoop et al., 2012) which found that individuals with depression made higher offers. Destoop et al (2012) interpreted this as a desire to avoid their offers being rejected; in the context of the SRH, this could be perceived as a mechanism by which to avoid the risk of rejection via greater adherence to prosocial norms, or as evidence of heightened generosity to increase your social value to others.

We also found that members of the Depressed group who scored above the moderate cut-off on the BDI (>18) rejected significantly more unfair, relative to fair, offers than Controls, in line with previous studies of the UG in depressed samples (Robson, 2020). Rejecting unfair offers has been characterised as a form of altruism, as the Responder must choose to endure afinancial cost in order to enforce social norms (Fehr & Gachter, 2002). Brethel-Haurwitz et al.(2016) compared performance during the UG to real-world altruism, with a sample of individuals who had all donated a kidney to a stranger. They found no difference in rejection rates between controls and donors, finding instead that rejection of unfair offers was closely correlated with self-reported frequency of socially-normative forms of altruism. These findingsindicate that rejection of unfair offers may be better characterised as a method of social norm enforcement, as opposed to a purely altruistic act. In Fehr, Fischbacher and Gachter's (2000)

theory of Strong Reciprocity, a person is a strong reciprocator if they are willing to sacrifice resources to enforce social norms, even when there are no material rewards for doing so. Strong Reciprocity encompasses both Positive and Negative forms of reciprocity, Positive reciprocity being "kind to those who are being kind" and Negative reciprocity being "punishing those who are being unkind". Our findings demonstrated an increase in both positive and negative forms of reciprocity in Depressed participants, potentially indicating a tendency towards Strong Reciprocity.

More recent work has examined the relationship between positive and negative forms of reciprocity and has argued that they in-fact represent distinct cognitive processes (Egloff, Richter & Schmukle, 2013), presenting a challenge to Strong Reciprocity theory. An alternative interpretation of our findings is that participants reject unfair offers to avoid the implicit inferiority of accepting. In Yamagashi et al's (2012) investigation of behaviours across a range of neuroeconomic tasks, they found that rejection of unfair offers in the UG did not correlate with prosocial behaviour across tasks and instead correlated with measures of assertiveness. This led them to conclude that rejection of unfair offers is not indicative of reciprocity preferences, but rather a desire to avoid being seen as unassertive and submissive towards the Proposer. Rejecting unfair offers in the UG could therefore be evidence either of prosocial upholding of social norms (Strong Reciprocity), or of a desire to avoid accepting a subordinate position. Both of these explanations reflect social status concerns, and in the context of the SRH could be interpreted as a way to increase one's social value to the group, or as a heightened aversion to decreasing rank. The concept that rejecting unfair offers represents a mechanism for communicating one's rank or utility to others would explain why rejection rates are higher during observation (Peterburs et al., 2017). Our finding of increased rejection of unfair offers in the Depressed group, in combination with higher offers to the In-group and to less

submissive players, would therefore seem to support the idea that sensitivity to social status and its management are features of depressed mood.

Imaging Findings: Risk and Group Membership

The AI and vmPFC were previously identified as the central components of a possible 'intuitive' system for recognizing social norm violations, in a meta-analysis from Feng, Luo and Krueger (2015). Based on the hypotheses of the SRH, we predicted that the Depressed group might show increased activation in these areas relative to our Control group, and increased activation in regions associated with social conflict monitoring such as the dACC, a pattern which was found in the only previous imaging study of UG in depression (Gradin et al., 2016). These predictions were not supported by the data; our whole-brain analysis found that the Depressed group exhibited increased activation in the superior frontal gyrus and anterior cingulate cortex (ACC) across conditions relative to Controls, while the ROI analysis found greater dmPFC activity in the Depressed group relative to Controls in the InGroup condition.

Superior Frontal Gyrus and ACC

Whole brain analyses found greater activation in the superior frontal gyrus (SFG) and ACC in the Depressed group across the task. With relevance to the current task, activation in the ACC has been related to processing of risk; in a gambling study by Fukunaga, Purcell and Brown (2018) activation of the ACC was found to reflect variance in the possible outcomes, and across subjects, variance-related activation within the ACC correlated with risk-aversion. Similarly, gambling studies which manipulate the level of risk have found the ACC recruited more during "high-risk" trials (Leijenhorst, Crone & Bunge, 2006), although this may also be indicative of response-conflict (Van veen & Carter, 2002). This relationship with risk may arise from the role of the ACC in error prediction; the error-likelihood hypothesis (Brown & Braver, 2005)

suggests that the ACC is sensitive to both the predicted likelihood and predicted consequence magnitude of a possible error. A study which found support for this theory observed greater activation in the ACC of risk averse individuals, and found this activation related to greater error sensitivity (Brown & Braver, 2007). Unsurprisingly then, both the ACC and SFG have been attributed a fundamental role in guiding decision making and action selection (Rushworth et al., 2004). In the context of the current task, where participants decided whether to accept or reject an offer, greater activation in the Depressed group might be indicative of heightened processing of risk and conflict relative to Controls, reflecting the increased importance of social interactions for this group. Overall, the observed activation in the ACC seems indicative of heightened sensitivity to social situations involving fairness concerns in depression, consistent with predictions of the SRH.

dmPFC

We found that the dmPFC was more activated in the Depressed group than Controls in response to In-Group offers. The dmPFC represents a key region of the Mentalizing network (Frith & Frith, 2006), and within this network has been chiefly associated with reasoning about the thoughts and intentions of others (see meta-analysis from Molenberghs et al., 2016). The dmPFC was previously characterised by Feng, Luo and Kruger as part of a 'deliberative' system which integrates and balances conflicting motivations of financial gain and social norm enforcement during the UG, based on its role in emotional regulation (Wager et al., 2008), which the authors reasoned was required to overcome the immediate appeal of economic reward, or immediate negative emotion in response to unfair treatment. Another way of conceptualising these conflicting motivations is in terms of valuation of behaviours; when making economic decisions, individuals make subjective valuations of behaviours which might result in rewarding outcomes (Kahneman & Tversky, 1984). However, these valuations are sometimes overridden by knowledge of social norms, when the individual places a higher

valuation on socially preferred behaviours (Fehr & Fischbacher, 2004). Apps and Ramnani (2017) performed a neuroimaging study which attempted to distinguish processing of subjective and socially normative valuations, by having participants perform a delay discounting task either according to their own preference (subjective valuation) or according to a previously learned "social norm" (normative valuation). They found that the dmPFC was specifically activated in relation to normative, but not subjective, reward valuations, in line with previous research which has implicated the dmPFC in social norms and conformity (Izuma et al., 2015; Nook & Zaki, 2015). This literature would seem to align with our finding that dmPFC activation was uniquely heightened during interactions with InGroup members, who would be subject to social norms, as opposed to OutGroup members, who would not. Overall, the observed activation in the dmPFC seems to indicate greater processing of social information and socially normative behaviour in the Depressed relative to the Control group, which is heightened particularly in towards the InGroup, aligning with the predictions of hypersensitivity to social interaction in this group.

Bilateral Occipital Pole and Superior Parietal Lobule

The results of the whole-brain analysis found evidence of greater activity in Depressed participants in the bilateral occipital gyrus, bilateral cuneus and bilateral lingual gyrus across analyses. These activations are not completely without precedent; a meta-analysis of UG imaging studies from Gabay et al. (2014) found the left lingual gyrus as one of the areas associated with the fairness contrast, and the bilateral cuneus for the response contrast(accepted vs rejected). Similarly, a study from Guo et al. (2014) also found the left cuneus associated with the fair over unfair contrast, and also with ratings of the unfairness of others with the increment of self-contribution. However, given that these regions have much more established associations with basic visual processing and facial recognition (Johns, 2014; Albohn & Adams, 2016) it is difficult to draw strong conclusions from these results. The whole

brain analysis also found greater activation in the superior parietal lobule (SPL) in the Depressed group; similar to the occipital pole, this region has well established associations outside of social and affective function, namely in visual perception, spatial cognition, and attention (Wang et al., 2015; Molenberghs et al., 2007). The SPL forms part of the mirror network (Gallese, Fadiga, Fogassi & Rizzolatti, 1996) which is recruited when observing and performing actions; while this network contributes to wider social functions, the role of the SPL appears to be chiefly in visuomotor representation (Molenberghs, Brander, Mattingley & Cunnington, 2010), and it is therefore challenging to draw strong conclusions regarding its involvement in the current task.

Limitations and Future Research

There are areas of improvement regarding the Group membership aspect of the protocol. The disadvantage of using the UG to investigate group preferences is that it provides a financial motivation to override group biases; Stagnaro et al. (2017) tested In-Group bias in the UG and a dictator game and found that group biases appeared only in the dictator game, concluding that participants desire to make acceptable offers in the UG was able to override their group-level preferences.

Despite this, we found several pieces of evidence which seemed to indicate stronger In-Group preferences in the Depressed group; at the neural level, our ROI analysis found greater dmPFC activation in the Depressed group relative to Controls during InGroup offers, while at the behavioural level, scores on the BDI and SBS correlated significantly better with InGroup offers than OutGroup offers. Previous studies have found conflicting evidence regarding in-group favouritism in low-status or low self-esteem individuals (Branscombe et al., 2002; Aberson, Healy & Romero, 2000), and there seems to be little evidence explicitly exploring this bias in depression. This may be a valuable avenue for future research with regards the

SRH; Hohman, Gaffney and Hogg (2017) proposed that feeling peripheral to one's social group can lead to feelings of self-uncertainty, which motivates an increase in in-group behaviours and biases. In the context of the SRH, we might therefore predict increased in-group specific bias in depression, as supported by our findings.

We found evidence indicating higher prosocial behaviour in depression, in line with the predictions of the SRH regarding improved ability to increase social value and avoid social risks. This included finding greater rejection of unfair offers and finding higher offer values in the Depressed group. However, this evidence could be more robustly interpreted in favour of the SRH if future work explored the motivations for these behaviours; existing research is conflicted over the purpose of rejecting unfair offers, between altruistic punishment of norm-violating behaviour, or a desire to avoid subjugating oneself to the Proposer. While Yamagashi et al. (2012) found evidence supporting the latter in healthy participants, there appears to be little research into distinguishing these motivations in depressed participants, and future research should replicate this cross-task design to investigate the motivations of this group. Similarly, finding higher offers in depressed groups has been suggested to be caused by heightened desire to avoid harm and rejection. This does not go against the hypotheses of the SRH, but future studies could investigate this further by including and controlling for measures of harm avoidance (Cloninger, 1993).

Overall, our results show support for the predictions of the Social Risk Hypothesis of Depressed Mood, finding higher offers and higher rejection of unfair offers in our Depressed sample, and a positive relationship between both of these variables and symptom severity. Our imaging results found greater activity in both the ACC and dmPFC in the Depressed Group; together these findings indicate greater sensitivity to social norm violations and greater processing of risk in this socially salient context. Moreover, both behavioural and imaging data indicated a sensitivity towards the In-Group in the Depressed sample, a context highly relevant

to social exclusion. Future research should distinguish the relationships of In-group and Out-group interactions with social status concerns and examine these behaviours in the context of depression.

CHAPTER 7. COOPERATION, PUNISHMENT AND SOCIAL NORMS IN A PUBLIC GOODS GAME

7.1. INTRODUCTION

A key feature of the Social Risk Hypothesis of Depressed mood (SRH)(see Chapter 1 for a detailed discussion) is its adaptive functionality. Allen and Badcock (2003) highlighted several core features of depressed mood which might be adaptive in a situation where one was at risk of exclusion, including hypersensitivity to social threat from others, sending signals to others that reduce social risks, and inhibiting risk-seeking behaviours – defined as those behaviours which could be perceived as confident or acquisitive. The purpose of this experiment was to test this prediction of the SRH by examining the presence of cooperation and punishment behaviours in clinically homogenous groups of Depressed and Control participants, using a well-established neuroeconomic task.

As discussed in Chapter 1, neuroeconomic games are an interdisciplinary body of experimental measures drawn from the fields of economics, psychology, and neuroscience, which apply principles of Game Theory (Nash, 1950) in social decision-making tasks. Amongst these, Public Goods Games (PGGs) have been utilised previously to examine cooperation in the presence of an incentive to defect. The task requires individuals to contribute resources to a group pot, which is then multiplied and split equally amongst the group. At an individual level, making zero contributions will produce the best outcome for any one player regardless of the actions of others (Olson, 2009) as they share in the public pot without expending resources themselves, termed “Freeriding”. However, at a group level, each player gains the most resources when they contribute all of their tokens into the public pot, thereby maximising the opportunity to multiply tokens.

The SRH posits that we determine our social status by the ratio between our value and burden to a given social group, termed Social Investment Potential (SIP). A group member who chooses to Freeride, contributing nothing to the group’s resources and gaining tokens at the

expense of others, represents a significant burden to the group. This strategy is therefore highly socially risky. Conversely, a group member who makes generous contributions provides value to the group, adopting a strategy with low social risk at their own personal expense and increased potential for personal loss. Examining the contribution strategies of individual players, alongside their clinical status, therefore provides an opportunity to examine the prediction that depressed mood will result in an inhibition of socially risky behaviour. Moreover, the inclusion of a punishment element in the task allows us to draw conclusions on the prediction of hypersensitivity to social threat signals.

Public Goods Games

Chapter 1 introduced Neuroeconomic Games, a category of social game based on Game Theory paradigms, which mimic real-life social interactions under controlled laboratory settings, and thereby allow social decision making to be studied experimentally. These include the Dictator Game and Trust Game, the Ultimatum Game (utilised in Chapter 6), and the Prisoner's Dilemma and Public Goods Game, amongst others. The Prisoner's Dilemma (PD) and Public Goods Game (PGG) are often addressed together within this literature, with the PGG sometimes characterised as an iterated, group version of the PD.

An important assumption within Game Theory is that of Utility Maximization, that is, that individuals seek to attain the highest level of satisfaction from their economic decisions (McCormick, 1997). Accordingly, the predicted Nash Equilibrium within a one-shot Public Goods Game, a zero-sum design in which participants contribute only once to the group pot, would be total Freeriding (Chu & Li, 1999). With regards to these assumptions, early research investigating cooperation in PGGs produced two key findings. Firstly, that in one- shot style games, contribution size is typically far greater than total Freeriding, on average around 40-60% of the optimum level (Ledyard, 1995). Significantly, this has been replicated cross-

culturally (Henrich et al., 2001) and up to stake sizes equating to three months income (Cameron, 1999). Secondly, in multi-shot games occurring over several rounds, contributions start at the same level but decrease gradually across rounds (Chauhuri, 2011). Subsequent research has focused variously on categorizing the main strategies adopted by players and the individual differences associated with them, understanding the role of punishment and rewards, and the development of theoretical models to explain the motivations behind players choices.

The most prevalent contribution strategy amongst players of both one- and multi-shot games is the conditional co-operator. This contribution type is one whose contribution to the public good positively and directly correlates with their beliefs about the contributions of others. Kurzban and Hauser (2005) performed one of the most comprehensive attempts to reliably characterize different contribution types in the PGG. They used 7 different versions of the PGGwith a sample of 84 participants and found that 96% could be classified as either conditional co-operators (63%), unconditional co-operators, who contribute over half of their endowmentregardless of the contributions of others (13%), or free-riders (20%), and that this classification was predictive of contribution levels in three subsequent neuroeconomic games.

Within the PGG, we can define success at the group level as the sustaining of a high level of cooperation, leading to a greater combined acquisition of resources. Several factors may influence the success of a group, one of which is punishment, which is discussed in more detail below. Other factors which may improve cooperation include the presence of intergroup competition (Tan & Bolle, 2007), a sense of similarity with group-mates (Gachter & Thoni, 2005) and lower population densities, which allow defectors and co-operators to coexist (Hauert, Holmes & Doebeli, 2006). Rapoport and Suleiman (1993) investigated the effect of heterogeneity of initial endowment, by giving some participants far larger sums than others. They found that members contributed the same proportion of their endowment regardless of its magnitude, but that homogeneous groups were more successful overall.

Neuroeconomic Games in Affective Science

The relevance of constructs such as altruism make neuroeconomic games obvious candidates for examining behaviours associated with affective dysfunction. However, their application in this area has produced inconclusive results, and the use of PGGs specifically remains extremely limited.

There are several examples of increased prosocial behaviour in depression (Destoop et al., 2012; Caceda et al., 2014; Ong et al., 2017). Partners with depressive symptoms make higher offers in the Ultimatum Game than their non-depressed counterparts (Destoop et al., 2012), more frequent reciprocal altruistic choices during Trust games (Caceda et al., 2014) and demonstrate higher levels of cooperation in the Trust Game compared to controls (Ong et al., 2017). Results such as these have been used to support theories of the link between pathological altruism and depression (Kaufman & Jauk, 2020), defined as "the willingness to irrationally place another's perceived needs above one's own in a way that causes self-harm" (Bachner-Melman & Oakley, 2016). However, these findings are by no means conclusive, and conflicting results from a range of neuroeconomic games have found decreased altruistic behaviour in depression (Zhang, Sun & Lee, 2012; Pulcu et al., 2013). Explanations for reduced prosociality in depression have included the possibility that associated anhedonia reduces the pleasure from interacting positively with others, or that these findings reflect an impaired ability to integrate affective and cognitive information when making social decisions (Robson, 2020).

Limiting our scope to the Prisoner's Dilemma (PD) and Public Goods Games, we find a similarly conflicting body of research. Sorgi and Wout (2016) investigated the relationship between cooperative behaviour and self-reported depressive symptoms using an iterated version of the PD (iPD). In this study, a subclinical population played three versions of the iPD with computer-programmed coplayers: one cooperative, one unbiased, and one predominantly

defecting. They found that greater severity of depressive symptoms was associated with more reliable cooperation with a cooperative coplayer, but more volatile cooperation with an unbiased or defecting coplayer. Conversely, Clark et al. (2013), found that scores on the Depression Anxiety and Stress Scale (DASS) correlated negatively with cooperative behaviours in both a PGG and PD. According to the SRH, depressed mood should precipitate low-risk attempts to increase one's social value, which might be best achieved through cooperative and altruistic behaviours. However, the most adaptive strategy will vary according to the specific social context and the behaviour or identity of coplayers, which may explain the variety of findings in this area.

The design of the above studies highlights two limitations common to the application of neuroeconomic games to affective science. Firstly, the exclusive use of subclinical or non-diagnosed populations. This distinction may be more important than it first appears; Alarcon and Forbes (2017) reporting on the relationship between age, depression and social function note a shift in the relationship between prosociality and depressive symptoms across the clinical to subclinical range, which they highlight for further research. Secondly, the use of computer-generated coplayers as opposed to genuine participants; while this allows experimenters to control the behaviour of agents, and thereby examine the response of participants to differently cooperative coplayers, it prevents naturalistic observation of behaviours that develop interactively between players and reduces the ecological validity of the task (Branas-Garza, 2011).

The current study aimed to address both issues by using participants with SCID-diagnosed MDD (First, Williams, Karg & Spitzer, 2015), and by forming groups of solely depressed or solely healthy participants. Core to the SRH is that the benefits one provides to the group should outweigh any perceived burden, if one's status is to be secure. We might then predict that contributions by depressed participants should be relatively high. Moreover, if we hypothesize

that individuals with depression are predisposed to view themselves as “burdensome”, this should further skew the size of contribution required to negate that burden.

Punishment in the Public Goods Game

Within the context of the PGG, punishing others is theoretically irrational from a purely economic standpoint. It reduces not only the immediate resources of the punishing player, but also the resources available for inclusion and multiplication in the group pot, thereby reducing the potential for future gains. However, previous literature has demonstrated that individuals frequently choose to punish others, even at their own expense, and that doing so is effective at increasing cooperation within the group,

In 2004, Fehr and Gachter performed a series of public goods games manipulating the identity of players (either playing multiple rounds together or varying the players randomly) and whether they had the option to punish. Across both identity conditions they found that in the absence of punishment, contributions declined sharply across rounds, quickly approaching full free-riding. After enabling the option to punish, contribution size doubled even before punishment had taken place and continued to climb, with full cooperation becoming the preferred strategy over 10 rounds. Variations of this design have found similar results; Miltenburg et al. (2014) performed a PGG where punishment could be assigned either individually, only by majority group decision, or only by unanimous decision. In this design the likelihood of punishment by group decision was far lower, and as such was less effective at promoting cooperation, even when the size of the punishment was greater. Gurerk, Irlenbusch and Rockenbach (2016) performed a repeated public goods situation in which participants could choose to play in one of two concurrently occurring PGGs, one with punishment options and one without. Initially, two-thirds of participants chose the punishment-free condition. Participants that chose the punishment condition imposed harsh sanctions on

free-riders and achieved almost total cooperation. Interestingly, however, across the course of the game, almost all participants who had started in the punishment-free condition opted to switch across to the punishment game, and contributed at the same level as the initial punishers.

There are two broad schools of thought in terms of the motivation of punishment in social groups. Fitness differential theory (Price, et al., 2002) proposes that humans punish in order to eliminate the differential advantage accrued by freeriding. According to this theory, punishment is motivated by a punitive sentiment that overwhelms the rational knowledge of its material cost. Several testable predictions can be made from this theory, for example that higher contributions to the group should correlate with higher likelihood of punishing others, as it is the high contributors who suffer most from the action of freeriders. The goal of punishment here is to negate the higher payoff received by the freerider. Reciprocity-based theories of punishment (Gintis, 2000) make similar predictions, however the motivation is subtly different. The purpose of punishment is not to reduce the payoff advantage received by the freerider per se, but to provide feedback on the violation of a social norm. This theory would therefore predict differences in the punishment strategies applied to in-group members, who are subject to such norms, and out-group members, who are not.

The option to punish improves cooperation and overall income (Fehr & Gachter, 2000). Crucially, those who do not punish are able to avoid the cost of doing so, but still share in any benefits associated with the punishment afflicted by others. Punishing can therefore be considered an altruistic action, as it enhances cooperation of the group, and group gains, at a personal loss for the punisher (Boyd, Gintis, Bowles & Richerson, 2003).

Depression and Punishment Sensitivity

Increased sensitivity to punishment, alongside reduced responsiveness to reward, is a well-documented feature of depression (Eschel & Roiser, 2010; Allen et al., 2018). One framework

for understanding the action of punishment sensitivity in depression is Gray's Reinforcement Sensitivity Theory (RST; Gray, 1970). The theory posits that there are individual differences in the sensitivity of the Behavioural Inhibition and Activation Systems, and that these differences underlie core features of personality and risk of psychopathology. Of most relevance here is the Behavioural Inhibition System (BIS), which is responsible for organizing the behavioural response to aversive stimuli, such as punishment. The response triggered includes an increase in arousal and attention, as well as inhibition of ongoing behaviours, and may involve goal-conflict resolution (Gray & McNaughton, 2000). In the context of the SRH, the purpose of such hypersensitivity might be to bias attention towards signals of potential risk. Several studies have reported significant positive associations between BIS reactivity and depressive symptoms; Hundt et al. (2007) reported greater BIS reactivity as being predictive of specifically anhedonic depression symptoms, while Pinto-Meza et al. (2006) reported BIS hyperactivity in both currently depressed and remitted samples. Recent studies have found that baseline BIS scores may be predictive of success of antidepressant treatments in depression (Allen et al., 2018).

Within the context of the Social Risk Hypothesis, we would expect depression to be associated with heightened sensitivity to signals of social threat. While social threat may take many subtle forms, being punished by a group member is an explicit expression of disapproval, with a high imperative that the behaviour should be changed. We therefore predict that punishment will have a greater effect on the contribution size of our Depressed group as compared to Controls. The SRH also predicts that depression is associated with the inhibition of social risk-taking, and more effective attempts to improve one's Social Investment Potential. As punishing others conveys a punitive sentiment, and additionally reduces the group's resources available for inclusion and multiplication in the group pot, we hypothesised that our Depressed group would administer less punishment compared to Controls.

Hypotheses

We conceptualise freeriding as socially risky within an establishing group, whereas cooperation mitigates social risk. We therefore made three hypotheses with regard to SRH; Firstly, Depressed groups will behave more cooperatively, seen as higher contributions and greater overall accumulation across rounds. Secondly, due to greater punishment sensitivity in this sample, punishment should be more effective at promoting cooperation in Depressed groups, seen as higher contributions following punishment. Thirdly, Depressed participants will punish less frequently, as this could constitute a negative and potentially risky social interaction.

7.2. METHODS

Participants

Full details of participant demographics, exclusion criteria and recruitment procedures can be found in Chapter 3. The current task was played in groups of five; two groups were removed due to participant dropout, bringing the total participant number to 50. Participants were 50 adults (mean age=46.28, range 21-74, female = 30) recruited from the MRC CBU volunteer panel. This comprised 25 Control participants (mean age=44.36, range 21-64, female=15) and 25 Depressed participants with SCID-diagnosed MDD (mean age=48.22, range 21-74, female=15). The Depressed group had an average Beck Depression Inventory II score of 25.44, falling within the moderate range (20-28), which was significantly different to the Control group average of 5.83 ($t(48)=8.31$, $p<.001$).

Protocol

The current task formed part of a larger protocol, detailed in Chapter 3. Participants completed the protocol in groups of five of the same clinical status (Depressed or Control). Participants

were seated with the group in an open testing room, allowing them to see their fellow group members (but not their screens), and were permitted to interact between tasks. For confidentiality reasons participants were not informed of the clinical status of the group; however, they were told that they had been grouped based on “trait similarities”.

Prior to the task, participants were given an information sheet detailing the task procedure (Appendix 7.1). This sheet was read aloud by the experimenter, and there was an opportunity to ask questions. Participants were also able to refer to this sheet during the task.

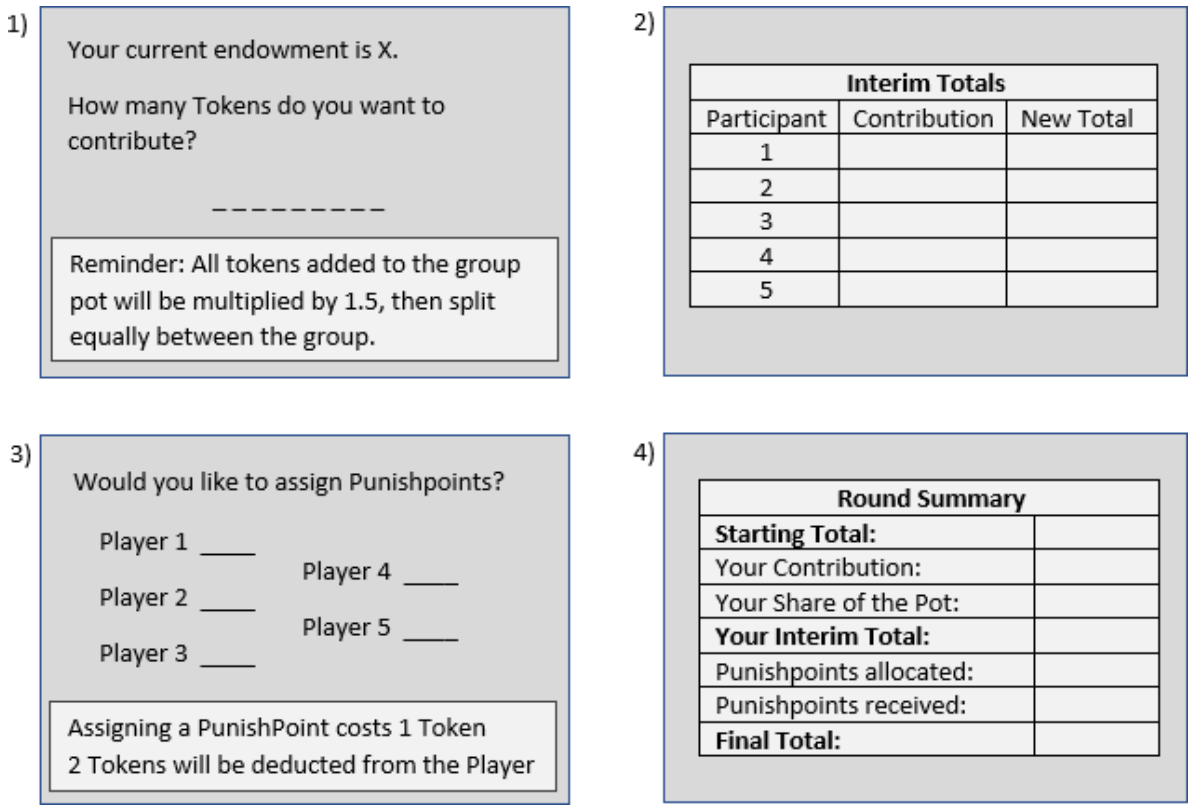


Figure 7.1. Simplified slides from a single round of the public goods game.

The experiment was executed on individual laptops, programmed using Z-tree (Fischbacher, 2007), a specialised software for performing group-based tasks such as the Public Goods Game. The task was a standard linear Public Goods Game of 10 rounds, with a punishment element.

At the start of the task, each participant was informed that they had been endowed with 20 tokens, which they were told to regard as having a value of £0.05 each. Each round contained four screens (Figure 7.1). In Screen 1, participants were asked to enter the number of tokens from their endowment that they wished to contribute to the "Group Pot". The rest would automatically be retained in their individual pot. They were informed that the total sum in the Group Pot would be multiplied by 1.5 and split equally amongst the group. In Screen 2, participants were shown a table detailing each group members contribution to the round and their updated total after receiving their share of the Pot. In Screen 3, participants were asked if they wished to anonymously assign a Punish Point to one of their fellow group members. There was a cost of one token to assign a Punish Point. Participants who received a Punish Point would have two tokens deducted from their total. In Screen 4, Participants were shown a summary of their performance during the round, including the number of punish points they had received and their updated total number of tokens.

Questionnaires

Full details of all social and affective questionnaires completed by participants can be found in Chapter 3. Five of these were included in the current analysis; the Beck Depression Inventory II (BDI; Beck, Steer & Brown, 1996) and Beck Anxiety Inventory (BAI; Beck, Epstein, Brown & Steer, 1988) were included as measures of affect, while the Hewitt-Flett Multidimensional Perfectionism Scale (MPS; Hewitt & Flett, 1990), Submissive Behaviour Scale (SBS; Allan & Gilbert, 1997), and the Striving to Avoid Inferiority Scale (SAIS; Gilbert, Broomhead, Irons & McEwan, 2007) were included as measures of social behaviour.

Data Analysis

For the primary analysis at the individual level, five variables were calculated for each participant across all 10 rounds; Final Total (the total number of tokens accrued by the

individual at the end of the task), Mean Percentage Contribution (mean proportion of tokens contributed as a percentage of the participants' endowment across all rounds), Mean Raw Contribution (mean number of tokens contributed across all rounds), Mean Percentage Punishpoints (mean number of tokens spent on allocating punishpoints to others, as a percentage of the participants endowment across all rounds) and Mean Raw Punishpoints (mean number of tokens spent on allocating punishpoints to others across all rounds).

Multiple comparisons were corrected utilising a Bonferroni correction. Independent sample t-tests were conducted to identify between-groups differences across these five key variables. To investigate the relationship between making contributions and allocating punishment, Pearson correlations were conducted between Mean Percentage Contribution and Mean Percentage Punishpoints (Keser & van Winden, 2000; Chaudhuri, 2011). Pearson correlations were carried out between the five key variables and five measures of affect and social status.

Percentage Contribution was also calculated for each individual at each round. Pearson correlations and a follow-up Univariate ANOVA were run to identify changes in Percentage Contribution across rounds. To investigate whether being punished increased subsequent contributions, Pearson correlations were run between Percentage Contribution and Punishpoints received in the previous round. To investigate whether contributions influenced the likelihood of being punished, Pearson correlations were run between Percentage Contribution and Raw Punishpoints received.

7.3. RESULTS

Outliers and Demographic Factors

An Outlier analysis found extreme values in the Mean Percentage Contribution, Mean Raw Punishpoints and Mean Percentage Punishpoints variables, in both the Depressed and Control

groups (Appendix 7.2). Z values were calculated for these variables and values +/-3 were excluded from analysis (Seo, 2006). Four of one-hundred and sixty-two data points were excluded across three variables (Table 7.1).

Variable	Clinical Group	Raw Value	Z Value
Mean Percentage Contribution	Depressed	100	3.06578
Mean Raw Punishpoints	Depressed	6.40	4.15704
Mean Percentage Punishpoints	Depressed	54.04	4.47306
	Control	30.93	4.07679

Table 7.1. Excluded data points

Limited previous research has indicated gender differences in contributions to the group pot (Vugt & Iredale, 2012). However, independent samples t-tests did not find significant differences between males and females on any of the five key variables either across or within groups, all t<1.36, all p>.18 (Appendix 7.3).

Contribution

Results of independent samples t-tests for the 5 key variables are presented in Table 7.2. Independent Samples t-tests did not find any significant differences between groups for the Mean Percentage Contribution (t(48)=-.33, p=.741) or Mean Raw Contribution (t(48)=.59, p=.552) variables. There was no significant difference between the Final Totals of the Depressed and Control Groups, t(48)=.03, p=.972.

	Controls		Depressed			
Variable	M	SD	M	SD	t statistic	Sig.
Final Total	41.58	17.69	41.36	26.16	.03	.972
Mean Percentage Contribution	.39	.18	.41	.19	-.33	.741
Mean Raw Contribution	10.45	3.32	9.81	4.13	.59	.552
Mean Percentage Punishpoints	.03	.04	.06	.11	-1.03	.306
Mean Raw Punishpoints	.91	.91	.91	1.32	-.01	.990

Table 7.2. Independent samples t-test found no significant differences between groups on the 5 key variables

Pearson correlations showed a significant negative relationship between Round and Percentage Contribution both across and within groups (Across; r=-.25, n=500, p<.001, Depressed; r=-.36, n=250, p<.001, Controls; r=-.12, n=250, p=.062), with contributions decreasing as more rounds were played (Figure 7.2). A follow-up Univariate ANOVA found a significant interaction between the effects of Round and Clinical Group on Percentage Contribution, whereby contributions in the Depressed group decreased faster across rounds than Controls ($F(1,480)=7.79$, $p=.005$), although there were no significant differences in Percentage Contribution in any of the individual rounds (Appendix 7.4).

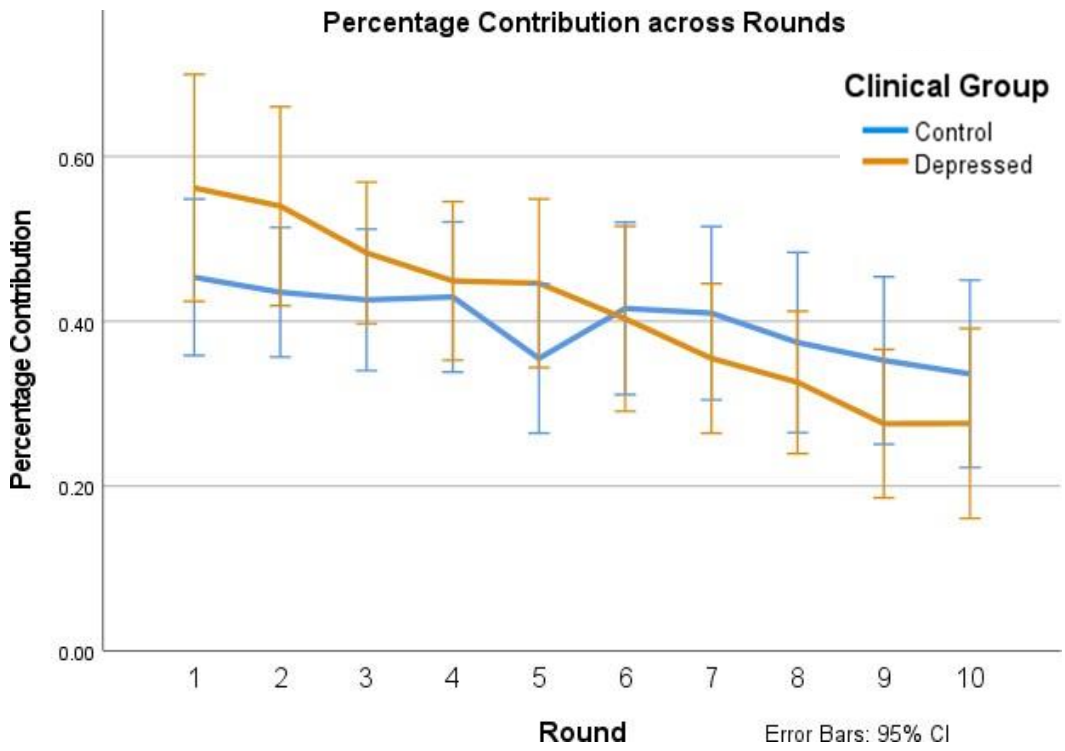


Figure 7.2. Depressed participants contributions, as a percentage of their total endowment, decreased faster across rounds than Controls.

Punishment

Who were the Punishers?

An Independent Samples t-test found no significant difference between groups on either the Mean Percentage Punishpoints (t(48)=-1.03, p=.306) or Mean Raw Punishpoints (t(48)=-.01, p=.990) variables, indicating that there was no significant difference between groups in the number of Punishpoints they allocated, or the proportion of tokens utilised for punishment (Table 7.2).

Pearson correlations investigated whether high contributors were also high punishers. In the Depressed group, there was a significant relationship between Mean Percentage Contribution and Mean Percentage Punishpoints (r=.53, n=25, p=.027). This relationship was not found in

the Control group (r=-.02, n=25, p=.933), and a Fischers r to Z transformation found that these correlations differed significantly between groups (z = 1.91, p=0.03).

Who received Punishment?

In both groups, the number of Punishpoints a participant received was significantly negatively correlated with their Percentage Contribution in that round (Controls; r=-.14, n=250, p=.023, Depressed; r=-.12, n=250, p=.047) indicating that individuals who cooperated received less punishment from their groupmates. The same relationship was not observed with the Raw Contribution variable (Controls; r=.06, n=250, p=.313, Depressed; r=-.01, n=250, p=.871), suggesting that the absolute material value of the contribution was not as important in determining punishment as the proportion of one's endowment contributed.

Pearson Correlations found that uniquely in the Control group, the overall mean number of Punishpoints received had a strong positive correlation with the overall Mean Percentage Punishpoints allocated (Controls; r=.58, n=25, p=.002, Depressed; r=.09, n=25, p=.681). The difference in the strength of this correlation between groups was found to be statistically significant (z=1.92, p=.03). Furthermore, a significant relationship was observed at the level of individual rounds, between the Raw Punishpoints allocated in one round and the Raw Punishpoints received in the following round, again uniquely in Controls (Controls; r=.23, n=225, p=<.001, Depressed; r=-.04, n=225, p=.511), although the strength of these correlations did not differ significantly between groups (z=.92, p=.18).

What effect did Punishment have on Contributions?

A variable was calculated to represent the change in raw contribution from one round to the next, Contribution Change. Pearson correlations found that, in the Depressed group, Contribution Change correlated negatively with punishment received in the previous round (r=-.17, n=225, p=.011) indicating that Depressed participants contributed less following

punishment. This relationship was not found in the Control group (r=.05, n=225, p=.493), however, the difference between groups was not significant (z=.72, p=.24). A follow-up Independent Groups t-test was conducted to compare Contribution Change in post-punishment trials between groups, in which punishment size was used as a weighting variable. This analysis found a significant difference between groups (t(294)=4.65, p<.001, d=.54) with Controls increasing contributions following punishment (M=.75, SD=4.77) and Depressed decreasing (M=-1.85, SD=4.82).

7.4. DISCUSSION

The findings of the current study did not support our three main predictions. Our primary hypothesis was that our Depressed group would contribute more to the public good as a way of reducing their risk of exclusion; we found that while individuals with depression made higher contributions than Controls initially, their level of cooperation decreased faster across rounds, and the overall average of their contributions was not higher. Our secondary prediction was that, due to heightened punishment sensitivity, the Depressed group would increase their contributions more than Controls following punishment, however, we found that the Depressed group actually decreased their contributions in response to punishment. Finally, our third prediction was that the Depressed group would administer less punishment than Controls, as this punitive action could be perceived as socially risky. We found no difference between the levels of punishment assigned by Control and Depressed groups, although we did find differences in patterns of punishment which are discussed here.

Trusting Others and the Risk of Contributing

Our finding that cooperation decreased faster in the Depressed relative to Control group is in line with the findings of a previous study from Clark et al. (2013) who found in a non-clinical sample that depressive symptoms correlated with lower contributions in a PGG. A possible

contributing factor to these patterns may be the role of trust. The existence of low levels of trust in Depression is well-established; levels of depressive symptoms correlate negatively withself-report measures of trust (Jasielska et al., 2019; Lin et al., 2020; Kim et al., 2012) and lowlevels of social trust have been found to be predictive of the development of Depression at 3- year follow-up (Fujiwara & Kawachi, 2008). Trust has a significant effect on interpersonal cooperation (Yamagashi, 1986), and is associated with making larger contributions in games involving public goods (Balliet & Van Lange, 2012). Ishi and Kurzban (2008) found that high trusters cooperated significantly more than low trusters in a PGG. Moreover, contributions by high trusters always exceeded low trusters, and increased over the course of the game.

These findings are not necessarily at odds with the Social Risk Hypothesis. Previously, Forgas (1998) found that individuals were less likely to cooperate and make reciprocal deals following a sad mood induction; in discussing these findings, Allen and Badcock (2003) comment that "the proclivity of the sad participants to avoid such behaviours, and their accompanying risk of exploitation, is consistent with our view that instead of capitalizing on highly risk-laden opportunities for potential social gains, depressed individuals behave in ways that reduce the risk of further social losses". We might therefore conceptualize trusting others as a risky decision (Cobb-Clark et al., 2019), particularly for those low in social capital. A possible interpretation for our findings then is that individuals with depression experience lower levels of interpersonal trust and perceive the risk that others will not cooperate with them as greater, and are therefore more cautious in their allocation of resources to the group.

Response to Punishment

Our second prediction, that depressed individuals would cooperate more following punishment than Controls, was also not supported, instead finding that the Depressed group reduced their contribution following punishment. These findings may be contrary to previous theories of

heightened sensitivity of the Behavioural Inhibition System in depression (Gray, 1970). A possible explanation for this finding might be that punishment increased the perceived social risk associated with the task, creating a desire to withdraw or disengage. The SRH posits that depressed mood precipitates withdrawal from reciprocal exchange interactions which confer a risk of exploitation and defeat. Thus, reduced contributions may have been the result of preferring to withdraw than to actively attempt to improve one's position following negative feedback (punishment). This would fit within the context of learned helplessness (Seligman, 1975), in which individuals perceive a low level of control over punishing events and therefore fail to address them. It might also reflect poorer strategy shifting abilities, previously reported in depression during the Iowa Gambling Task (Must et al., 2006).

Punishment and Social Norms

Our third prediction was that the Depressed group would administer less punishment than Controls, due to the potential social risk of such a punitive action. This prediction was not supported, as we found no difference between the overall punishment levels of the groups. However, a significant correlation was found in the Depressed group between levels of punishment and contribution, that was not found in the Control group, and the strength of correlation differed significantly between groups. This behaviour pattern aligns with reciprocity-based theories of punishment, which posit that the purpose of punishment is to provide feedback on the violation of a social norm (Gintis, 2000), and that those who exhibit such norms (through contribution) will also enforce them (through punishment). Punishment of norm violations reliably enhances cooperation within groups (Balliet, Mulder & Lange, 2011) at a cost for the punisher, and is therefore often characterized as altruistic. Accordingly, individuals who punish in PGGs are rated as more trustworthy, group-focused and worthy of respect than non-punishers (Barclay, 2006) and are more likely to subsequently receive help from others via increases in reputation (Santos, Rankin & Wedekind, 2010). Neilssen (2008)

reports that individuals who chose to invest the most into punishing others were more likely to be chosen as partners in a subsequent trust game and were transferred more money in that game. Altruistic punishment might therefore be an effective way of improving one's reputation and Social Investment Potential by taking the burden of enforcing social norms which benefit the wider group.

Limitations and Future Research

Previous literature posits that anti-social punishment may occur in PGGs as a mechanism of protecting oneself against potential competitors (Rand & Nowak, 2011). Anti-social punishment is conceptualised as punishing out of a desire to achieve "payback" on someone who punished you. Participants were not told during the task who had chosen to punish them, however, it would have been possible for a determined player to deduce this by having observed the interim totals of their teammates, and then observing their starting totals in the following round. Because assigning a Punishpoint incurred a cost of one token, and this deducted two points from the receiver, observing a reduction of any odd number of tokens would indicate a player had punished in the previous round. We found that, uniquely in the Control group, the overall number of Punishpoints received had a strong positive correlation with the overall Percentage Punishpoints allocated; this correlation was absent in the Depressed group, and differed significantly between groups. This analysis is speculative given the design of the task, however, differences in punishment motivation may provide an interesting avenue for future research on altruism and social behaviour.

The current study tested participants in clinically homogenous groups. This aspect of the protocol was designed to examine whether cooperative behaviour preferences would emerge in the Depressed group when the potential of Control subjects freeriding was removed. However, the investigation of hyper-altruism by Pulcu (2013) found that depression was

associated with greater fluctuations in altruistic behaviour as a factor of recipient characteristics, relative to controls. This is supported by a previous study from Kupferberg et al. (2018), in which participants played a simple neuroeconomic paper-folding game against a partner. They could choose either a competitive or cooperative payment scheme and were either informed that their partner had the same diagnosis as them (Depressed or Control) or were not given the diagnosis status. When participants with depression were informed that theirpartner shared their diagnosis, 70% chose the competitive scheme, whereas when their partners diagnosis was unknown, only 13% chose to compete. By comparison, in dyads of healthy controls, 33% chose to compete. These findings are reflective of a study of responses in a social gaming tournament which found that depression selectively inhibits upwards, but not generalized or downwards, competitiveness (Szücs et al., 2020). In the current task, participants were informed that they had been grouped with others possessing “similar traits”, which may have influenced their propensity for altruistic behaviour. This interpretation is strengthened by findings from the Ultimatum Game (Chapter 6) which found that the Depressed group made lower offers to those with higher Submissive Behaviour Scores relative to themselves. These findings highlight the importance of considering the heterogeneity of social relationships, and are in line with the SRHs prediction that depression should be associated with an adaptive tendency to minimize risks differently in different social contexts (Allen, Gilbert & Semedar, 2004).

This study could have been improved by including a measure of trust, such as the Generalized Trust Scale (Yamagishi & Yamagishi, 1994), which would have allowed us to test the possibility that lower than predicted levels of cooperation in the Depressed group stem from a reluctance to trust others. Previous research has observed low levels of trust in depressed participants utilizing self-report measures (Jasielska et al., 2019), however, trust as a concept

is generally under-researched, and future investigations might consider whether trusting others represents a socially risky strategy.

Overall, our predictions regarding increased cooperation in the Depressed group were not supported. However, the SRH does not specifically predict increases in prosocial behaviour in depressed mood, but that individuals are able to increase their social value and reduce their social burden more effectively, and exhibit adaptively increased sensitivity to signals of social threat. We found evidence that tentatively supports these predictions and warrants further investigation; individuals with depression may punish and collaborate in equal measure as a way of upholding social norms and thereby increasing their value to the group; their contributions to the group may decrease faster over time due to a reluctance to risk trusting others; they may react to punishment by sending signals of withdrawal and defeat rather than actively shifting strategy. Future research should address the concept of trust, and the influence of heterogeneity of rank status of others in social interactions.

CHAPTER 8. SOCIAL RISK TAKING IN DEPRESSION: THE BALLOON ANALOGUE RISK TASK

8.1. INTRODUCTION

The defining tenet of the Social Risk Hypothesis of Depressed Mood (SRH; Allen & Badcock, 2003) is the adaptive inhibition of social risk-taking behaviours in those with critically low social status (See Chapter 1). Social risk-taking constitutes an action or behaviour which confers the possibility of a negative outcome for the social status of the individual; choosing to make an unpopular decision, for example, would be a socially risky decision. The inhibition of risky or impulsive behaviours more generally has obvious adaptive advantages, however, inhibition of specifically social risk-taking often constitutes behaviours such as submissiveness signalling, whose advantages might be more obscure. According to the SRH, these are only adaptive when the individual is at a critically low social investment potential (SIP), i.e. the ratio between ones social value and social burden is imbalanced such that the perceived risk of exclusion from the group is imminent, serving to protect the individual from further reductions in SIP.

Risk Taking in Depression

Chapter 1 provides a discussion of the mechanisms by which reduced social risk-taking in depression might arise according to the SRH, and a review of supporting literature. This includes evidence of reduced appetitive motivation in depression, reduced reward sensitivity, and memory biases which overweight the likelihood of failure, amongst others. The current chapter will focus not on these underlying mechanisms, but on evidence of their behavioural outcome, reduced risk-taking.

Self-report measures of risk-taking have indicated increased risk-taking in depression, reporting a positive relationship between overall risk-taking and depression relevant constructs such as anhedonia (Pushkarskaya et al., 2019), as well as specific positive relationships between depression and recreational risk-taking (Kodaraimi & Fati, 2016). Elsewhere, studies surveying

real-world behaviour have used metrics such as gambling or dangerous driving habits to quantify "riskiness", and many of their findings also indicate a greater propensity for risk-taking in depressed individuals. Depression and psychological distress has been associated with risky driving behaviours (Scott-Parker et al., 2011), physical violence (Pesa, Cowdery, Westerfield & Wang, 1997), problem gambling behaviour (Takamatusu, Martens & Arterberry, 2015) and risky sexual behaviour (Coyle et al., 2019; Kosunen, Kaltiala-eino, Rimpela & Laippala, 2003; Sales, Spitalnick, Crittenden & DiClemente, 2011).

A complicating factor in the use of self-report and real-world metrics of risk-taking is the possibility that adoption of these "risky" behaviours is elevated in individuals with depression as a coping strategy. Smoking is frequently used as evidence of a propensity for risk-taking due to its negative health consequences (Ert, Yechiam, Arshavsky, 2013), however nicotine is a psychostimulant with a known effect on several neuroregulators influencing mood (Leonard, et al, 2001). Depression is also frequently concurrent with other risk-factors for drug-use or smoking, for example delinquency (Leas and Mellor, 2000), making directional conclusions on the basis of these findings challenging.

Behavioural measures of risk-taking provide an opportunity to avoid such concerns. These measures often take the form of neuroeconomic games involving some aspect of gambling and payoff, and include, amongst others, the Holt and Laury Task (2002), the Game of Dice (Brand, Fujiwara et al. 2005) and the BART (Lejeuz et al., 2002). A more thorough review of neuroeconomic games and their applications to affective science can be found in Chapter 1. In the Holt and Laury Task (2002) participants make a series of gambles, in each round choosing between a risky gamble with high payoffs, or a safe gamble with lower payoffs.

Testing of depressed participants on this task has found comparable risk preferences and value sensitivities to those of healthy controls (Chung et al., 2017). In the Game of Dice

(Brand, Fujiwara et al. 2005) participants maximise their capital by correctly guessing the outcome of a throw of a virtual dice. Risky players can guess a single outcome, resulting in the largest gain, while risk-averse players may choose to guess two or three outcomes, with lower potential gains. Use of this task with depressed participants has found suicidality positively associated with risky decisions in this game (Deisenhammer et al., 2018). In addition to these tasks, previous studies have utilised measures designed to test decision making under ambiguity, most notably the Iowa Gambling Task (Bechara, Damasio, Damasio & Anderson, 1994). These have produced similarly conflicting results, with Smoskiet al. (2008) reporting that depressed participants were better able to avoid risky cards than controls, while Must et al. (2006) report that they make fewer such advantageous choices. Investigations utilizing behavioural measures of risk-taking have therefore produced conflicting results in relation to risk-taking in depression.

Although risk-taking in a broad sense has been well investigated in depressed samples, specifically social risk-taking is less well studied. This may be problematic; a recent review of the risk-taking literature from Bran and Vaidis (2019) highlights the need for a more domain-specific approach to risk-taking assessment, drawing on literature which has found high domain specificity in risk-taking preferences (Hanoch, Johnson & Wilke, 2006; Weber, Blais & Betz, 2002). Cobb-Coyle, Damann and Kettlewell (2019) examined risk-preferences across financial, health-related, and social domains, and found no general tendency for depressed individuals to engage in more or less risky behaviours, but rather, that the specific domain was of greater importance. In line with the theoretical context of this thesis, studies investigating domain-specific risk taking have indicated that social risk is of particular relevance in depression; Andrews, Foulkes, Bone and Blakemore (2020) developed a questionnaire measure of concern for health and social risk behaviours (HSRQ), finding greater concern forsocial risk was positively related to depressive symptomology.

Overall, there is a general trend towards increased risk-taking in depression. Surveys of real-world behaviour find higher engagement in risky behaviours in depressed populations, especially in adolescents, however, the difficultly of controlling relevant societal and ecological factors makes conclusions about the underlying constructs unreliable. This study will investigate risk-taking specifically within the social domain, utilizing an adapted version of the well-established neuroeconomic assessment of risk taking, the Balloon Analogue Risk Task (BART).

The Balloon Analogue Risk Task

The Balloon Analogue Risk Task (BART) (Lejuez et al., 2002), is a behavioural measure of risk-taking under experimental conditions. It was originally developed to investigate riskiness in adolescence, in response to the drawbacks of existing self-report measures which relied on guardian reports of risk-taking and suffered a response-bias whereby adolescents often down-played their willingness to engage in risky behaviour. As the task was not developed with the purpose of investigating social or altruistic behaviour it is not considered a traditional neuroeconomic game, despite sharing many similar characteristics, and the alterations made in this study are some of the first to apply it to these questions. In the game, participants press a response key to inflate a computerized balloon. Reward tokens are accrued in proportion to the size of the balloon, so there is an incentive to inflate the balloon as large as possible through repeated presses, or “pumps”. However, risk exponentially increases the more the balloon is inflated, as the balloon may “pop” at any time, losing all of the accrued tokens. Participants may save (or “bank”) their tokens at any time; however, this returns the balloon to its minimum size. The typical dependent variable is an adjusted BART score representing the average number of pumps across unexploded balloons.

Evaluations of the BART have found it has high validity in predicting real-world risk-taking behaviour (Lejuez, et al, 2003). Performance on the BART has been shown to correlate with trait measures of risk-taking and impulsivity (Hunt et al., 2005) as well as real-world behaviour such as drug abuse and alcohol usage (Aklin et al., 2005), and gambling and smoking in both adolescent (Lejuez et al., 2003) and adult samples (Lejuez et al., 2002). The BART shows high test-retest reliability (White, Lejuez & Wit., 2008), and has been found to have better retest reliability than other behavioural tasks used in the assessment of risk-taking such as the Delay Discounting Task and Iowa Gambling Task (Xu, Korczykowski, Zhu & Rao, 2013). Skeel, Neudecker, Pilarski and Pytlak (2007) investigated the combined utility of behavioural and self-report personality measures in the prediction of risk-taking behaviours, and found that the BART accounted for a significant proportion of the unique variance in risky behaviours, beyond that accounted for by personality variables. Unlike many other behavioural measures of risky decision making, the BART does not require participants to memorize reward contingencies, and there is no ambiguity in the size of risk, therefore providing a more direct measure of risk-taking.

Considering the large body of research linking engagement in real-world risk-taking behaviours with depression, there is extremely little research in which the BART has been applied to affective disorders. Heilman et al. (2010) investigated the effect of emotion and emotional regulation strategies on risk-taking during the BART and found that naturally occurring negative emotions increased risk aversion, but that this effect could be reduced by incidental use of cognitive emotional regulation strategies. In addition, Hevey, Thomas, Laureano-Schelten, Looney and Booth (2017) investigated BART performance amongst a sample of participants with depression, compared to a matched control group. They found

that the control group made a significantly higher number of pumps during the BART than the depressed group, indicating greater propensity for risk-taking. Moreover, higher levels of depressive symptoms were significantly correlated with lower numbers of pumps amongst depressed participants. The authors also investigated punishment sensitivity, measured as the average decrease in pumps following a loss trial. In line with previous literature indicating heightened punishment responsiveness in depression (Eschel, 2010; Allen et al., 2018) they found a greater decrease in pumps following a loss trial in the depressed group compared to controls.

In the current study, a modification was made to the BART to allow investigation of the social dimension of risk-taking; participants played the game once for themselves, and once for their 'team', a group of fellow participants who were present throughout the task (although unable to directly observe the players screen) and with whom they had previously completed a collaborative task. In the context of Social Risk Hypothesis (SRH), the degree towhich a participant inflates the balloon to accrue more tokens when playing with the team's money is an index of 'social risk' – it could produce greater payoffs for the team, but with a greater risk of losing the team's money. The degree of social risk can be mitigated by cautious play, settling for smaller wins and banking smaller sums to avoid potential losses. Examining individual player strategies alongside their clinical status therefore provides anopportunity to examine our prediction that depressed mood will result in the inhibition of specifically socially risky behaviour.

There are examples existing in the literature of the BART being conducted within a social context, which find a reduction in risk-taking behaviours in healthy populations. The presence of a reference person displaying facial expressions of anxiety (Parkinson, Phiri & Simons, 2012) or even just being observed by a peer (Kessler, Hewig, Weichold, Silbereisen & Miltner, 2016) has been associated with greater risk-aversion in the task.

Furthermore, using the BART in a more naturalistic context, by adapting it for smartphone use, revealed that players responded in a riskier manner in sessions where they reported being alone (Maclean, Pincus, Smyth, Geier and Wilson, 2018). These studies illustrate the sensitivity of responses on the BART to social contexts, making it an appropriate measure for adaption here. A crucial distinguishing point between these studies and the current task is that, in previous investigations, the risk being taken is not explicitly one which confers status or regard; resources won or lost are the players own. The current study modifies the BART such that players have the potential to win or lose resources belonging to the group, presenting an unambiguous risk to one's social standing and approval.

Hypotheses and Aims

Building on the Social Risk Hypothesis of Depressed Mood (Allen & Badcock, 2003) we hypothesised that depressed individuals would exhibit greater risk aversion in the social condition of the Social BART (expressed as a greater number of balloon pumps per trial) relative to the individual condition, compared to the profile of never-depressed controls. We also addressed a secondary hypothesis, based on the findings from Hevey et al. (2017), that our depressed sample would exhibit greater punishment sensitivity than never-depressed controls, indicated by a lower mean number of balloon pumps in post-loss trials compared to post-win trials across task conditions.

8.2. METHODS

Participants

Full details of participant demographics, exclusion criteria and recruitment procedures can be found in Chapter 3. Participants were 62 adults (38 female, range 18-74, mean=45.77yrs) recruited from the MRC CBU volunteer panel. They comprised 32 Control participants (20 female, age range 18-64, mean=44.85yrs) and 30 Depressed participants (18 female, age range 21-74, mean=47.44yrs). The Depressed group had an average BDI score of 27.61 (falling near the top of the moderate range, 20-28), which was significantly different to the Control average of 5.45 ($t(60)=-9.67$, $p=<.001$).

Protocol

The BART task was presented as part of the larger protocol detailed in Chapter 3. This involved performing a number of tasks as a group, most importantly, participants had previously collaborated on a Public Goods Game (PGG; Chapter 7) with four other participants who were present in the same room throughout. The experience of collaborating with, and gaining knowledge of, their fellow participants was designed in-part to increase theecological validity of the social component of the current task and to foster team- membership. The groups were clinically homogenous, comprising either exclusively Depressed or Control participants. Participants were not explicitly informed of this but were told they had been grouped with people who saw the world similarly to themselves. Prior to these tasks, participants had also completed several questionnaires related to mood and socialrank (see Chapter 3).

The Social BART Task

Participants were seated in a communal testing room with four fellow participants and the experimenter. The Social BART was administered on individual testing laptops, which were positioned such that the screen was visible only to the individual participant. The task was programmed using PsychoPy, a specialised software for experimental psychology, and the visual layout based on Peirce (2019). Prior to the task, participants saw an on-screen information page (Appendix 8.1) detailing the task procedure and monetary value of the tokens. Crucially, participants were informed that they would play two versions of the task, "Individual" and "Social"; in the Individual condition they were playing only for themselves, whereas in the Social condition they were playing for the group and would share their wins with the other group members. They were informed that these wins would be publicised to the rest of the group the following day. This screen was read aloud by the experimenter, and there was an opportunity to ask questions.

Participants played the game once in the individual condition and once in the social condition, with the order counterbalanced across participants. After the initial information screen, participants saw a second screen informing them of which condition they were playing, and an indicator of the condition remained on-screen throughout the task.

Participants pressed the space key to inflate, or "pump", a red balloon presented on the screen, to accrue tokens, with bigger balloons accruing more tokens. When they wished to save, or "bank", their tokens for that balloon they pressed the enter key, and the balloon would then return to its minimum size. Instructions for the "pump" and "bank" keys remained on-screen throughout. Also on-screen was a running total for the current balloon, aswell as a total for the task (Figure 8.1). The balloons were programmed to pop at between 1 and 120 pumps, with an average breakpoint of 60. This was achieved utilizing the same method as Lejuez et al., in which an array of numbers 1-120 was constructed, and a number chosen from the array in each round, with the balloon exploding if the number 1 was selected.

As numbers were not replaced into the array after selection, the risk of explosion increased with each pump. If the balloon popped before a player had banked their tokens they were presented with a screen which informed them that the tokens had been lost. The dependent variable is adjusted average pumps, representing the average number of pumps across all balloons in that condition which did not explode (Lejuez et al., 2002) and this was calculated at the individual level for both Individual and Social conditions.

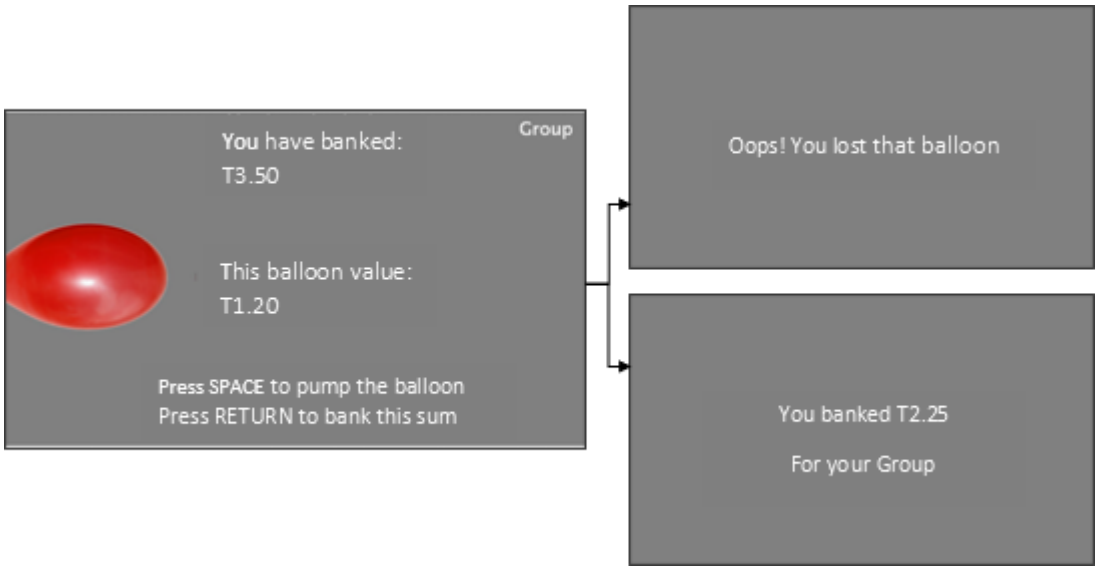


Figure 8.1. The BART as it was presented to participants, including loss and bank screens.

Questionnaires

Participants completed a range of questionnaires relating to mood and social rank as part of the thesis protocol (for full details, see Chapter 3). Six of these questionnaires were included in the analysis of the current task; two measures of affect, The Beck Depression Inventory-II (BDI; Beck, Steer & Brown, 1996) and Beck Anxiety Inventory (BAI; Beck, Epstein, Brown & Steer, 1988), three measures relevant to social rank, the Submissive Behaviour Scale (SBS;Allen & Gilbert, 1997), Involuntary Subordination Questionnaire (ISQ; Sturman, 2011) and

Striving to Avoid Inferiority Scale (SAIS; Gilbert, Broomhead, Irons & McEwan, 2007), and one measure of perfectionism, the Hewitt-Flett Multidimensional Perfectionism Scale (MPS: Hewitt & Flett, 1990).

Data Analysis

For our primary analysis, an adjusted BART score was calculated at the individual level for both Individual and Social conditions, representing the average number of pumps across all balloons in that condition which did not explode (Lejuez et al., 2002). Paired samples t-tests were run within Clinical Groups to identify differences in risk-taking between the social and individual conditions. Independent samples t-tests were run to identify differences between Depressed and Control groups in either condition, followed by a two-way repeated-measures ANOVA. To address our hypothesis of increased punishment sensitivity in the Depressed group, a 3-way factorial ANOVA was run to between Clinical Group, Condition (Social vs Individual) and Outcome of Previous trial (Loss vs Win). Finally, Pearson correlations were run between mean number of pumps and measures of depressive symptoms (Beck Depression Inventory, Beck Anxiety Inventory) and questionnaires relevant to social rank (the Socially-Prescribed Perfectionism subscale of the Hewitt-Flett Perfectionism Scale, Submissive Behaviour Scale, the Insecure subscale of the Striving to Avoid Inferiority Scale, and Involuntary Subordination Questionnaire).

8.3. RESULTS

A two-way repeated-measures ANOVA with the adjusted mean number of pumps per trial as the dependent variable, Condition (individual, social) as the within-subjects factor and Clinical Group (Depressed, Control) as the between-subjects factor found no main effect of

Condition (F(1,60)=1.450, p=.233, ηp^2 =.024). Consistent with our hypothesis, there was a significant interaction between Group and Condition, F(1,60)=10.241, p=0.001, ηp^2 =.146, (Figure 8.2).

Breaking this interaction down, paired samples t-tests revealed that the Depressed group made significantly fewer pumps in the social condition compared to the individual condition, t(26)=3.47, p=.002, d=.668), whereas within the control group, there was no significant difference between conditions (t(34)=1.37, p=.180, d=.232). Furthermore, independent samples t-tests showed that the Depressed group made significantly fewer pumps during the social condition than did controls (t(60)=2.22, p=.030, d=.570), but that there was no significant difference between groups during the individual condition (t(60)=.27, p=.79, d=.068).

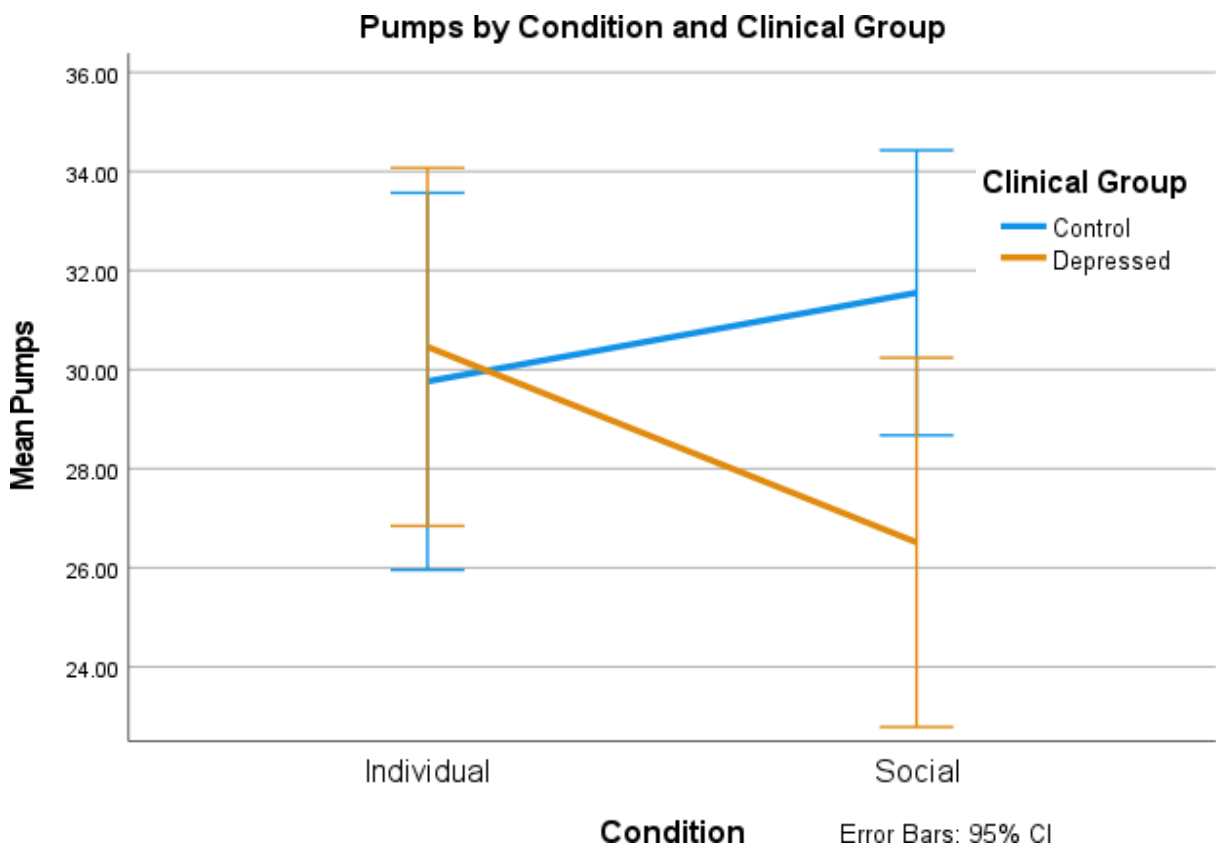


Figure 8.2. Estimated marginal means showing a significant interaction between Clinical Group and Condition

Punishment Sensitivity

To investigate our second hypothesis, that Depressed individuals would be more risk-averse than Controls following punishment, i.e. loss trials (Hevey et al., 2017), we generated an additional variable, Change in Pumps, which represented for each participant the average change in number of pumps following a loss. A two-way repeated measures ANOVA with Change in Pumps as the dependent variable, Condition (individual, social) as the within-subjects factor and Group (Depressed, Control) as the between-subjects factor found no significant interaction between Group and Condition ($F(1,60)=.00$, $p=.954$, $\eta p^2 =.000$), but did find a significant effect of Condition ($F(1,60)=14.37$, $p=.000$, $\eta p^2 =.188$) (Figure 8.3).

A follow up paired samples t-test found that groups made fewer pumps in the individual compared to social condition (t(60)=3.83, p=.000, d=.479).

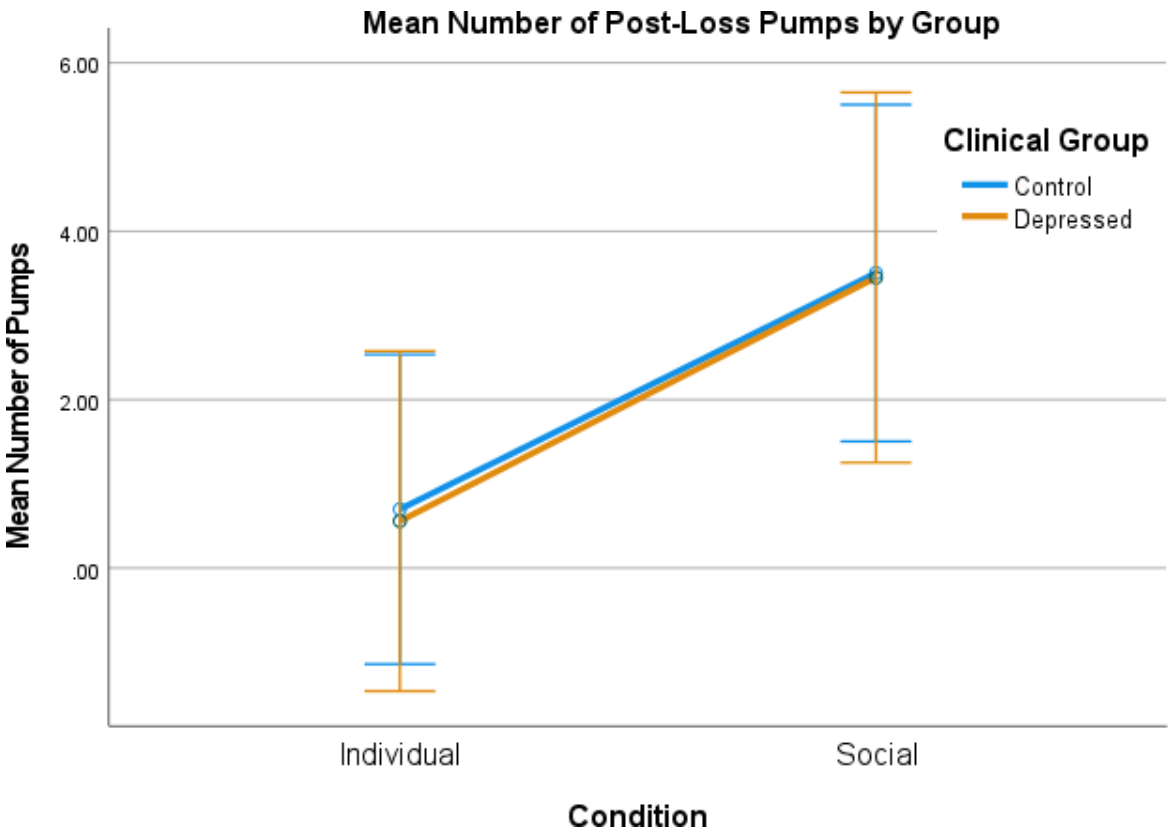


Figure 8.3. There was a significant effect of Condition on the number of post-loss pumps, with both Groups making fewer Pumps in the Individual Condition

Behavioural Covariates

Across Groups, none of the questionnaire measures showed a significant correlation with pumps made either in the Group or Individual task. Within groups, the Depressed sample showed a significant negative correlation between scores on the Socially-Prescribed Perfectionism (SPP) subscale of the Hewitt-Flett Perfectionism Questionnaire and mean number of pumps made in the social BART ($r(27)=-.41$, $p=.035$).

8.4. DISCUSSION

This thesis aims to investigate the predictions of the Social Risk Hypothesis of Depressed Mood (SRH; Allen & Badcock, 2003), to extend our understanding of social functioning in the etiology of depression. The current study aimed to evaluate the extent to which depressed individuals show a specific reduction in social risk-taking, measured as performance during a computerized risk-propensity task. In line with the predictions of the SRH and our hypotheses, the results suggest that depression is associated with a lower propensity specific to *social* risk-taking. This was indicated firstly by a lower number of pumps in a social risk condition relative to controls, secondly that this difference was not replicated in the individual condition, and thirdly that within the Depressed group, number of pumps in the social condition was significantly lower than in the individual condition. We also identified asignificant relationship between Socially-Prescribed Perfectionism (SPP) and risk aversion inthe social condition that was specific to the Depressed group.

Our findings are supportive of the Social Risk Hypothesis of Depressed Mood (SRH; Allen & Badcock, 2003); core to this theory is aversion for social risk-taking, and hypersensitivity to social threats. Previous research has rarely addressed social risk as a specific construct,

however, our findings align with a previous investigation into the SRH by Olive and Brewer (2014), in which depressed individuals completed self-report measures of social risk-taking and rank. The authors found that levels of depressive symptoms were correlated with a lower willingness to engage in risky behaviour, and with a perceived fall in social status. The current study tested this construct using a behavioural assessment of risk-taking, allowing us to control for self-presentation bias and the confounding effects of adoption of risky behaviours as coping strategies in depressed populations. These findings contribute to our understanding of the interaction between social experience and depression, particularly in the context of rising incidence of depression worldwide (Liu et al., 2020) and its associations with increasing problematic social media use (Shensa et al., 2017), and increasing instability of our social hierarchies (Saavedra-Rodríguez & Feig, 2013).

We did not find any significant differences in punishment sensitivity between groups, therefore not replicating the results of Hevey et al. (2017). A possible underlying cause may be the effect of antidepressants in the sample. Antidepressants may increase behavioural activation and impulsivity (Harada, Sakamoto, Ishigooka, 2008); the Depressed group had inconsistencies in medication status, with 13 of the 27 participants reporting current medication, whereas all of the clinical participants in Hevey et al. were receiving antidepressant medication. It is possible therefore that there was an effect of medication on sensitivity to negative outcomes, leading to differences in punishment sensitivity across the Depressed group.

Two possible confounding factors in use of the BART with clinical participants are the role of executive function and delay discounting. There is evidence to suggest that executive function has a contribution to risk-taking behaviour on the BART (Capone et al. 2016) and that working memory capacity specifically is associated with better performance and lower variability of performance on the BART in healthy adolescents (Blair, et al. 2018). Depressed

individuals have been found to have impairments in working memory (Christopher & MacDonald, 2010) as well as other executive functions (Channon & Green, 1999). Depressed individuals have also been found to show a preference for short-term rewards (Pulcu et al., 2014). In the BART, the greater future payoff of a large balloon may be subject to more discounting by depressed samples. It is possible that due to the flattening of reward-responsivity in depression (Allen, et al., 2018) the prospect of a monetary reward was insufficient to motivate our Depressed group to take risks which might obtain that greater future reward. Importantly, however, these limitations would apply equally to both the individual and social conditions of the task and would therefore struggle to explain the social specificity of the observed risk aversion.

Previous research suggests that framing of the BART as a "Loss" context, an opportunity to avoid losing money, may affect propensity for risk-taking (Gabriel & Williamson, 2010). However, there is disagreement over the direction of this effect, as literature suggest that a "Loss" framing may make participants either more risky (Benjamin & Robbins, 2007) or less risky (Gabriel & Williamson, 2010). In the current task, participants were informed that this was an opportunity to *win* tokens, a gains context, which has not been shown to have any significant associations with risky-behaviour, however the terminology in the instructions could have been expanded to include the potential for loss, thereby removing any directionality in the framing of the task.

In conclusion, this study found a lower propensity for social risk-taking in our Depressed group, compared to healthy controls and non-social risk-taking. These findings have important implications within the context of the current thesis, as they provide validation of one of the key predictions of the Social Risk Hypothesis of Depressed Mood. Moreover, these findings are the first to use a specifically social behavioural measure of risk-taking in this clinical group. Future research in this area should investigate the replicability of these

findings in cross-cultural samples, and utilise emerging methodologies for assessment of risk-aversion.

CHAPTER 9. GENERAL DISCUSSION AND FUTURE DIRECTIONS

9.1 THESIS OVERVIEW

The work reported in this thesis aimed to extend our understanding of social processing in clinical depression, as characterised by a diagnosis of Major Depressive Disorder (MDD) according to the DSM-5, by testing hypotheses generated from socio-evolutionary theoretical frameworks of depression, with particular reference to the Social Risk Hypothesis of Depressed Mood (SRH; Allen & Badcock, 2003). The investigations described in the previous chapters address existing questions in the neural and psychological literature by applying novel protocols and utilising neuroeconomic games in a unique cross-task design. This work will hopefully inform and refine theoretical accounts of depression, and the use of social functioning as a transdiagnostic marker for affective disorders more broadly.

Chapters 2, 4 and 5 investigated the neural response to self-discrepancy, within the context of socio-evolutionary theories which conceptualise affect as a socially homeostatic mechanism, with particular reference to the role of the “social pain” network in the brain. Chapters 6, 7 and 8 investigated the predicted behavioural outcomes of such discrepancies, with emphasis on social risk-taking and cooperation. This final discussion chapter will review the experimental findings from these empirical chapters and discuss how they might inform our characterisation of social functioning in depression and its aetiology. Finally, this chapter will outline limitations of this work and discuss potential avenues for further research.

9.2 REVIEW OF MAIN FINDINGS BY CHAPTER

Chapter 1 provided a general overview of Evolutionary Theories of Psychological Processes, with emphasis on the SRH (Allen & Badcock, 2003). Additionally, this chapter discussed current debates regarding the neural basis of social-rank processing and outlined how the use of neuroeconomic games in this thesis was placed to address these questions.

Chapter 2 described how neuroimaging data collected by Dalgleish et al. (2017) was reanalysed to investigate whether discrepancies between self-perception and social-rank feedback are processed distinctly from feedback valence. We found evidence that positive discrepancies were associated with increased activation in the right precentral gyrus and left medial frontal cortex, while negative discrepancies were associated with a fall in activation in regions of the dorsal striatum. The chapter went on to describe how these findings relate to current debates regarding social rank processing, and how the subsequent protocol would build on these results.

Chapter 3 described the main protocol of the thesis, which is unique in generating a cross-task dataset and in its utilisation of a group-induction design, in contrast to previous studies using strangers or computer-automated players. It also explored the hypothesis that depression is associated with systematic social processing biases by characterising the two participant samples, finding that our Depressed sample scored significantly higher on all measures of maladaptive social functioning, including Involuntary Subordination, Submissive Behaviour, Striving to Avoid Inferiority and Interpersonal Sensitivity.

Chapters 4 and 5 investigated the neural responses to self-discrepancies and social feedback. Chapter 4 explored the presence of discrepancies between actual and desired self-concepts and investigated the overlap between neural regions associated with self-discrepancy and social status. In line with previous research, we found that our depressed sample reported larger discrepancies between Actual and Ideal self-concepts. Across groups, neuroimaging data

revealed that during Large, relative to Small, discrepancies, increasing self-reported depressive symptoms (BDI) scores were associated with activations in the posterior and midcingulate gyrus (at the whole brain level) and vmPFC (at the ROI level), while in the Depressed group, perfectionism was found to correlate with activity in the dorsal Anterior Cingulate Cortex (dACC) and left Anterior Insula (AI), possibly supporting a role for this matrix in monitoring internal evaluations of one's social value relative to an ideal point. Across conditions, there was a main effect of group observed in the posterior and midcingulate gyrus, being more activated in Depressed participants relative to Controls.

In Chapter 5 the concept of discrepancy was expanded to interpersonal discrepancies – the differences between one's self-perception and the perceptions of others – with the purpose of identifying neural regions that might constitute a Sociometer (Leary et al., 1995). The whole-brain analysis found, in the Control group, activation in the middle cingulate gyrus associated with increasing negativity of discrepancy, as well as deactivation of the posterior insula during both positive and negative discrepancies, which was deactivated uniquely during positive discrepancies in the Depressed group. Our ROI analyses found that the dACC was deactivated in the Depressed group during both positive and negative discrepancies, but during positive discrepancies only in Controls, although there was no significant interaction between groups.

Chapters 6, 7 and 8 utilised neuroeconomic games to investigate the behavioural predictions of the SRH relating to social risk-taking. Chapter 6 involved the Ultimatum Game, a paradigm which allows us to observe cooperative behaviour and responses to unfairness, and in our protocol incorporated an in-group/out-group element. We found that the Depressed group made higher offers to others and rejected unfair offers more frequently, indicating a preference for reciprocal behaviour and a willingness to enforce social norms, both of which might increase one's social value in line with the predictions of the SRH. Moreover, the Depressed group exhibited greater activation in the ACC throughout, potentially indicating hypersensitivity to

this socially salient context. Interestingly, several pieces of evidence indicated a particular sensitivity towards in-group interactions; Depressed participants exhibited greater activity in the dmPFC in response to in-group offers relative to Controls, while our behavioural analysis found that measures of submissiveness and depressive symptoms correlated positively with in-group offers, significantly more than with out-group offers. In-group interactions are particularly salient for one's social rank and affiliative relationships, making these findings relevant for the SRH. Moreover, we found evidence that Depressed participants were sensitive to the relative submissiveness of their coplayers, making higher offers to those less submissive than themselves.

Chapter 7 investigated cooperative behaviour in a group context during a Public Goods Game, a paradigm that has not been widely utilised with clinical samples previously. With relevance to the findings of the UG, the Depressed group showed a correlation between levels of contribution and punishment which indicated a preference for exhibiting and enforcing social norms. Our prediction that Depressed participants would attempt to reduce their burden on the group by making higher contributions was not supported, however, we considered whether this might be rooted in elevated perceptions of the risk of others not reciprocating, as well as previous literature suggesting that Depressed individuals are selectively more competitive with other Depressed individuals. With reference to the findings of the UG regarding relative submissiveness, we discussed whether risk taking in depression might be expressed asymmetrically towards those of higher and lower status.

Finally, Chapter 8 described a novel social adaptation of the Balloon Analogue Risk Task (BART), a behavioural measure of risk-taking. In support of the predictions of the SRH, the Depressed group entered significantly fewer pumps in the social condition relative to the individual condition, and significantly fewer than controls.

In sum, our behavioural findings overall produced support for the predictions of the SRH, indicating greater social risk aversion in the Depressed group. We found that, rather than employing a strategy of universal cooperation, the Depressed group exhibited a preference for adhering to and enforcing social norms of reciprocity, which is particularly pronounced in in-group interactions. These findings were reflected in our imaging analysis, which found heightened sensitivity in response to norm violations and in-group interactions in the dmPFC. While the characterisation of the dACC and AI as a neural sociometer was not directly supported, we did find evidence indicating a role in the processing of discrepancy and self-salience. The current chapter will discuss these findings within the framework of evolutionary theories of depression and affective disorders, and consider their implications for further work in this area.

9.3. IMPLICATIONS WITHIN THE CURRENT FIELD

Risk-Taking and Cooperation

During the Pleistocene period (2.6m-12,000 years ago) membership of a social group conferred access to several resources crucial for evolutionary fitness, for example mate selection, food and shelter (Nowak & Highfield, 2011). Chapter 1 discussed socio-evolutionary theories of affective disorder which have sought to explain how the psychological mechanisms underlying these disorders might have functioned to maintain inclusivity in a social group. The Social Risk Hypothesis of Depressed Mood (SRH; Allen & Badcock, 2003) posits that depressed mood reduces the risk of social exclusion by increasing an individual's sensitivity to social signals, increasing submissive signalling, and reducing social risk-taking. These mechanisms predispose the individual towards low-risk, predictable social interactions which impart small gains in Social Investment Potential (SIP) while avoiding risky competitive or acquisitive interactions which carry the possibility of large gains or losses.

This thesis found support for this prediction, with our Depressed sample showing greater risk aversion during a social adaptation of the Balloon Analogue Risk Task (BART) than Controls, being more cautious with group resources than their own. This task is one of the first to behaviourally examine social risk-taking, which has previously been under-researched as a distinct construct (Bran & Vaidis, 2019) and is more often investigated using self-report measures (Olive & Brewer, 2014). Greater sensitivity to risk was also indicated in our neuroimaging findings; the Ultimatum Game (UG) was the only task presented here in which participants underwent scanning whilst making a social decision (whether to accept or reject another's offer). The Depressed group displayed significantly more activation in the superior frontal gyrus and anterior cingulate cortex throughout this task than Controls, regions which have been associated with both the appraisal and aversion to risk (Galvan et al., 2013; Brown & Braver, 2007; Fukunaga, Brown & Bogg, 2012; Fukunaga, Purcell & Brown, 2018).

Building on the predictions of the SRH, we hypothesised that risk aversion in our Depressed group might be expressed via greater cooperative tendencies, contributing more to the group to increase their social value and avoid punishment. We did not find this was supported, in line with previous studies which demonstrate reduced cooperation following sad mood inductions (Forgas, 1998) and in subclinical depression (Clark et al., 2013). These findings do not contradict the SRH, as displays of cooperation or selflessness do not always constitute the most risk-averse course of action, particularly in a paradigm such as the PGG where contributing requires trust in your fellow participants to reciprocate. Trusting others might not be adaptive in socially risky situations (De Cremer, 1999) and accordingly, low levels of trust are well-documented in depression (Jasielska et al., 2019; Lin et al., 2020; Kim et al., 2012). Similarly, the risks and benefits of cooperating likely vary according to the identity of the receiver; being seen cooperating or behaving submissively towards a low-ranked individual or out-group (Yamagashi et al., 2012) might confer more risk than benefit. We may therefore predict that

depressed mood should not be associated with more or less collaboration *per se*, but rather, with greater fluctuations in collaborative behaviour as a function of contextual or relational indicators of risk (Allen, Gilbert & Semedar, 2004). In support of this, in the UG, we found that the offers made by the Depressed group to in-group members varied as a factor of the difference in their Submissive Behaviour Scale scores (SBS; Allan & Gilbert, 1997), making higher offers to those who were less submissive, and lower offers to those more submissive. This finding was unique to the Depressed group, indicating heightened sensitivity to indicators of social rank such as submissiveness, or perhaps greater weighting of these indicators when making social investment decisions. These findings point to the heightened importance of relative social comparisons and perceptions of social context in guiding social behaviours in depression. This is in line with the limited number of previous behavioural studies investigating socio-economic decision making in depression, which have found that depressed participants show greater sensitivity to information about the submissiveness or relative status of their partners when making contribution decisions (Hokanson et al., 1980; Kupferberg et al., 2018). Together, these findings point to a strategy of risk avoidance in depression which is more sophisticated than purely altruistic or collaborative behaviours and is sensitive to social contextual factors.

Another important contextual factor in determining whether a decision is socially risky or not might be the social norms of the group one is operating within. Altruistic and collaborative behaviours present a challenge to the previously accepted wisdom that humans are purely selfish agents (Nash, 1950), and several theories have emerged attempting to explain the motivation of such behaviours (Rabin, 1993; Bolton & Ockenfels, 2000). Influential amongst these is the theory of Strong and Weak Reciprocity (Fehr, Fischbacher and Gachter, 2000); “Weak” Reciprocity constitutes a strategic decision, based on calculated expectations of future returns (Blanco et al., 2014), whereas “Strong” Reciprocity reflects an intuitive, evolved

preference for prosociality and reciprocity with prosocial others (Fehr & Schmidt, 1999). Strong Reciprocity encompasses both Positive and Negative forms of reciprocity, that is, responding in kind to both prosocial and antisocial treatment. In turn, this reinforces the purpose of reciprocity-based punishment to provide feedback on the violation of a social-norm. Those individuals whose motivation for punishing others is to enforce social norms should also then adhere strongly to cooperative norms themselves (Gintis, 2000). We found this pattern exhibited uniquely in the Depressed group across both neuroeconomic games; in the PGG, higher contributions correlated with higher levels of punishment assigned to others, while in the Ultimatum Game (UG), the Depressed group made higher offers than Controls and were more likely to reject unfair offers. This pattern of behaviour in the UG has previously been attributed to social norm enforcement; Brethel-Haurwitz et al. (2016) found that rejection of unfair offers was closely correlated with self-reported frequency of socially-normative forms of altruism. Providing feedback on the violation of a social norm, through punishment or rejection, enhances cooperation within social groups (Balliet, Mulder & Lange, 2011), at a cost for the individual. Those who shoulder that burden are therefore viewed more positively by their groupmates (Barclay, 2006) which translates to preferential treatment and collaboration in subsequent tasks (Neilssen, 2008; Santos et al., 2010). Enforcing social norms might therefore provide an effective way of building one's reputation and encouraging affiliative signals from others (Milinski et al., 2002). Moreover, this method of increasing ones SIP does not rely on existing affiliative relationships, making it appropriate for individuals with low levels of social support, as is often reported in depression (Rueger et al., 2016) and dovetails with the predictions of the SRH in maintaining group inclusivity despite potential cost to self-esteem.

This "social norm" interpretation of our findings is strengthened by the specificity of our results to the in-group; Gintis' (2000) reciprocity theory predicts that strategies of norm enforcement

will differ between in-group members, who are subject to such norms, and out-group members, who are not. We found that in-group offers, but not out-group offers, were significantly higher in the Depressed group than Controls, and that in-group offers correlated with scores of Submissiveness and Depressive Symptoms significantly more than out-group offers (SBS; Allan & Gilbert, 1997, BDI-II; Beck, Steer & Brown, 1996). Heightened sensitivity to in-group social interactions would align with the tenets of the SRH, as these interactions are more relevant to one's risk of social exclusion. Additionally, the SRH hypothesises that when signalling to reduce social threat, depressed mood is associated with a shift from engaging in high-risk interactions which might be competitive or exploitative, towards less risky interactions within relationships which are already well-established. In-group interactions might fall within this second category, as group membership confers preferential treatment for co-members (Tajfel, 1970). Similarly, individuals who are bound by the same social norms as ourselves are likely more predictable, reducing the possible variance in the outcomes of social interactions. Past research specifically relating to depression and in-group biases is limited, but would seem to support our proposed link; Major, Sciacchitano and Crocker (1993) found that unfavourable in-group comparisons were related to lower self-esteem and depressed affect, while out-group comparisons were not. More recently, Roberts and Burleson (2013) found that lower social connectedness was predictive of stronger in-group preferences.

Furthermore, this interpretation is reinforced in the neuroimaging analysis. A co-ordinate based meta-analysis of fMRI studies during the UG identified two networks; an 'intuitive', automatic system based in the AI and vmPFC implicated in recognizing social norm violationsand a 'deliberative' system based in the dmPFC involved in balancing these automaticresponses against economic interests, likely via emotion regulation (Feng, Luo & Kreger, 2015). Literature suggests that the dmPFC is particularly involved in socially normative decision making (Apps & Ramnani, 2017) and conformity (Nook & Zaki, 2015). We found

that activation in the dmPFC was significantly higher in our Depressed sample than Controls during In-group offers in the UG, suggestive of greater processing of norm violations in this status-salient context. These results seem to reflect an adaptive increase in the processing of social norm violations and social mistreatment, that is especially sensitive with regards to in-group interactions.

In sum, we found evidence of a specific aversion to social risk taking in our depressed sample, in support of the predictions of the SRH, that may be best characterised in the context of greater sensitivity to the social or relational context of the interaction. We found evidence that group membership is one such contextual factor, as our depressed sample exhibited heightened sensitivity towards in-group interactions and social mistreatment, and a stronger tendency to enforce in-group social norms, that was observable at both the behavioural and neural levels. These findings arguably support the SRH, as in-group interactions are particularly salient with regard to social exclusion, and enforcing social norms might represent an effective method of increasing one's social value. In-group bias and its relationship with depression and risk-taking has not been widely investigated previously, and these results suggest that group membership and social norms should be integrated into future research regarding socio-evolutionary theory.

The Sociometer, Discrepancy, and Perfectionism

The SRH posits that depressed mood is a response to critically low Social Investment Potential (SIP); the ratio between one's social value and social burden to a given group. One of the proposed features of depressed mood is hypersensitivity to social signals of risk, which aides in avoiding further reductions in SIP by increasing attention to indications of possible loss encounters. According to Leary and Baumeister (2000), signals of rejection and inclusion are tracked by a neural "Sociometer", which monitors our social rank, and this is then experienced as self-esteem (phenomenologically the same as SIP). This is sometimes characterised as an

"alarm system" (Eisenberger & Lieberman, 2004) which detects discrepancies from our ideal homeostatic set-point, and mobilises emotional, behavioural, and perceptual mechanisms to rectify them. Previous imaging research has pointed to the dACC and AI as a possible neural basis for such a sociometer, given their roles in social pain (Lieberman & Eisenberger, 2015; Eisenberger et al., 2003) and expectancy violation (Bush, Luu & Posner, 2000). Accordingly, activity in these regions seems to be heightened in individuals with depression (Silk et al., 2013; Yttregahl et al., 2018) and has been associated with reductions in self-esteem (Eisenberger et al., 2011). One of the goals of the work in this thesis was therefore to investigate, not just the neural response to valenced social information, but specifically to information indicating the presence of a discrepancy.

Our findings provide partial support for the theory that this matrix is involved in processing discrepancies, and that this activity is altered in depressed mood. In the Social Feedback task, we found deactivation of the AI across discrepancy types in Controls, but deactivation during positive discrepancies only in the Depressed group, although there was no significant interaction between groups. These findings are similar to those of Schie et al. (2018), who found insula deactivation during positive feedback in individuals with low self-esteem. Importantly, activation of the AI has been associated with processing of social prediction errors (Xiang, Lohrenz & Montague, 2013), implying that our findings may indicate differential processing biases for social discrepancies, with Depressed participants exhibiting a bias away from positively valenced discrepancies. These biases may have relevance to the positive self-processing bias that is well-established in control samples (Taylor & Brown, 1988; (Alicke & Govorun, 2005) and which seems to be absent in depression (Dunn et al., 2009). In the absence of a significant interaction between groups in this task, these conclusions are tentative and should be used as a springboard for further research regarding valenced biases in the processing of social discrepancies. In the Actual/Ideal task, our behavioural findings showed support for

the prediction that Depressed individuals perceive greater discrepancies between their Actual and Ideal self-concepts, in line with previous research (Johns & Peters, 2012; Bruch, Rivet & Laurenti, 2000). Our neuroimaging data found that the dACC and left AI were associated with increasing self-perfectionism during Large Discrepancy trials, compared to No-discrepancy trials, again only in the Depressed group, although there was no significant interaction between groups. This indicates a role for these regions in the processing of discrepancies between an individual's ideal set-point and their actual self-concept, and may indicate that these are particularly sensitive in perfectionistic depressed individuals. The relationship with perfectionism is interesting, as errors are thought to be particularly salient for this group because they serve to optimise future behaviour (Barke et al., 2017). Perfectionism may therefore be a moderating factor when it comes to sensitivity to discrepancy in depression. We found that self-orientated perfectionism and socially-prescribed perfectionism correlated with all of our self-report measures of affect, Submissiveness and Interpersonal Sensitivity. Moreover, in the BART, self-orientated perfectionism correlated with reduced social risk-taking, uniquely in the Depressed group. Conceptualising perfectionism as a heightened sensitivity to discrepancies, which are a trigger for homeostatic affective processes, might provide insight on the transdiagnostic relevance of perfectionism in affective disorder.

Also, in relation to discrepancy, we found activations in the middle cingulate gyrus (MCg) across tasks; in the Social Feedback task, the MCg was associated with increasing negativity of discrepancies, while in the Actual-Ideal task, the MCg was associated with increasing BDI score during the Large>No Discrepancy contrast. This region has an established relationship with the processing of pain (Maarawi et al., 2007; Hotta et al., 2017), fear (Levar et al., 2017) and anxiety (Chan et al., 2019). The observed activations might therefore indicate increased fear or anxiety associated with depressive symptoms in response to discrepancies, in line with

the theoretical predictions discussed in this thesis, and provide preliminary evidence that this region may also be involved in the experience of social pain.

Many socio-evolutionary theories of affect integrate homeostatic principles, by conceptualising the mechanisms of the condition as being triggered by a discrepancy from an ideal set-point. In this thesis we investigated the neural response to discrepant social feedback and reflection on self-discrepancies in a group of Depressed and Control participants. We found that the AI was differentially deactivated in these groups in response to social feedback according to the valence of the discrepancy, showing lower activation in response to positive discrepancies in the Depressed group. When reflecting on self-discrepancies, the Depressed group exhibited heightened activation in the dACC and AI that correlated with levels of perfectionism.

Our findings suggest a bias towards under processing of positive social discrepancies, which is strengthened by the results of our UG analysis. This is reflective of the SRHs conceptualisation that depressed mood potentiates a “err on the side of caution” approach to social processing, which involves biasing inferences from social feedback. Our findings also provide evidence that the dACC/AI matrix is involved in the processing of self-discrepancies, and raise the question of how perfectionism might inform this theory.

9.4. CHALLENGES AND OPPORTUNITIES

Generating appropriate social behaviour requires a myriad of complex perceptual and behavioural processes, including simulating the minds of others, attending to and integrating contextual information, and the flexible application of interpersonal strategies. The disruption to these functions observed in affective disorders (Panchal, Kaltenboeck & Harmer, 2019) has relevance for understanding their aetiology, and for the development of transdiagnostic treatment approaches. However, assessing social behaviours in an ecologically valid and controlled way presents significant challenges for researchers, with many previous studies

relying on self-report questionnaires or interviews (Kwak, Pearson & Huettel, 2014). Neuroeconomic games may provide an answer to this issue, by mimicking real-life, dynamic social interactions, within strategic scenarios which operationalise aspects of decision-making. However, their use requires further refinement; in their review, Robson et al. (2020) conclude that a clearer profile of the expected results of these games within healthy control samples is needed, particularly if they are to be utilised in neuroimaging paradigms. Improved standardisation and consistency across various aspects of these games, such as inclusion of non-social computerised conditions, or knowledge of opponents, would be beneficial in this regard. Two criticisms regarding the current use of neuroeconomic games were addressed by this thesis; firstly, the use of clinical samples may help to resolve existing conflicts arising from the inconsistent use of subclinical or non-diagnosed populations (Alarcon & Forbes, 2017). Secondly, the use of real-life participants and a group-priming context, as opposed to computer generated coplayers or strangers, is more ecologically valid, by allowing dynamic and reciprocal behaviours to emerge. Future research should consider the potential of neuroeconomic games for examining the effects of intervention on clinical symptoms (Grecucci et al., 2013) and for investigating the functional connectivity of networks involved in social processing (Gradin et al., 2015). Furthermore, their use in transdiagnostic clinical approaches, as a behavioural measure of constructs within the Research Domain Criteria framework, warrants further consideration.

Much of this thesis has focused on the concept of risk-taking, although research in this area is still in its early stages and would benefit from further work investigating social risk in clinical depression. However, ecological assessment of risk-taking also presents methodological challenges for researchers; in a comprehensive review of the risk-taking literature, Bran and Vaidis (2019) highlight the importance of realism in risk-taking tasks, and particularly the need for tasks which elicit greater arousal and emotionality. De-Juan-Ripoll (2018) describes

how this could be achieved with the use of Virtual Reality; the authors suggest an immersive virtual environment in which the subject must reach a point as quickly as possible, and then choose a route, selecting between traversing shorter, more dangerous paths or longer, safer paths. Virtual Reality has previously been applied effectively in socially relevant scenarios, for example in Virtual Reality Exposure Therapy for social phobia (Powers & Emmelkamp, 2008), which provides a promising foundation as a tool for investigating social risk.

Future Opportunities

We found that perfectionism was correlated with behavioural measures of social risk-taking as well as self-report measures of affect and social function. This is unsurprising, given that perfectionism is a transdiagnostic process that is robustly associated with a range of psychopathologies, including social anxiety, OCD and eating disorders (Maricutoiu, Magurean & Tulbure, 2019; Egan, Wade & Shafran, 2010). Slaney et al. (2001) conceptualised adaptive and maladaptive presentations of perfectionism; adaptive perfectionists set high self-standards, but maladaptive perfectionists have high standards alongside heightened perceptions of their discrepancy from that standard. This type of perfectionism might therefore be thought of as hypersensitivity to discrepancies from a set point, which is associated with increased affective distress and behavioural attempts to rectify the discrepancy, in line with the characteristics of a homeostatic mechanism. Recent research has indicated that the relationship between perfectionism and symptomology is moderated by self-esteem (Puttevils et al., 2019; Cokley et al., 2018; Zhang & Cai, 2012). Perhaps then perfectionism could be thought of as an adaptive sensitivity which may subserve homeostatic processes, but which becomes maladaptive in particular contexts. Preliminary work trialling cognitive behavioural treatments for perfectionism has shown substantial transdiagnostic value, resulting in increased self-esteem and decreased intolerance of uncertainty, and decreases in symptoms of OCD and eating disorders (Kothari et al., 2019). Future research might attempt to validate the relationship

between perfectionism, risk-taking and discrepancy discussed here, and theoretical work which seeks to explain transdiagnostic processes from the perspective of homeostatic and adaptive mechanisms should consider how best to characterise the role of perfectionism in this context.

We found several pieces of evidence indicating that depression is not associated with more cooperative behaviours per se, but with greater variations in cooperation according to social factors such as group membership, relative submissiveness and beliefs about others. Previous studies of depression have discussed altered cooperation as a social deficit or difficulty (Clark et al., 2013), however, future research could more closely consider relational and contextual factors which might make reduced cooperation the more adaptive approach. For example, appearing submissive to a lower-ranked individual conveys an implicit inferiority (Yamagashi et al., 2012), which may explain the effect of social observation on such interactions (Peterbus et al., 2017). Kupferberg et al. (2018) found that individuals with depression were more competitive when they knew their partner was also diagnosed with depression, possibly indicating a tendency to capitalise on interactions with individuals perceived to be lower risk. These findings were reflected in our Ultimatum Game task, where we found that the Depressed group made lower offers to individuals with higher Submissive Behaviour Scale (SBS) scores than themselves; this might indicate an implicit assumption that submissiveness is indicative of low rank, and accordingly reduced offers. These factors highlight the possibilities for future research which involves manipulation of the identity of coplayers, for example the inclusion of rank information or kin interactions. Another relevant factor might be the size of the perceived risk; in a trust game, Zhang, Sun and Lee (2012) found that depressed individuals did not make more altruistic responses than controls, however, they showed greater responsiveness to changes in the risk of a deception being made known to their partner. Future research might usefully identify relevant contextual social factors according to their ability to indicate the riskiness of a social decision.

Our findings indicate that our depressed sample showed a preference for adhering to and enforcing social norms, which we interpreted as a way of increasing ones social value. Future research should attempt to validate this finding and consider its implications in the context of the SRH. Interestingly, modelling approaches have suggested that punishment of norm violations is more effective at promoting norm internalisation than rewarding norm adherence (Gavrilets & Risherson, 2017) which underlines the importance of considering how punishment and non-cooperation might be socially adaptive. This is especially true in light of our findings regarding the heightened importance of in-group interactions in our depressed sample. We interpreted this within a socio-evolutionary framework which would conceptualise in-group interactions as more salient regarding social exclusion concerns. In this context, perhaps enforcing in-group social norms serves to accentuate commonalities with other group members, increasing the likelihood of group maintenance. More research is needed with both clinical and subclinical samples in investigating adherence and enforcement of social norms in depressed mood and clinical depression. Future theoretical work might integrate group membership as an important determinant in social-risk behaviour.

Future research should also consider the implications of the SRH for psychotherapeutic interventions. Previously, Sloman (2008) has discussed the promotion of self-assertion and healthy dominance behaviours in the treatment of depressed patients, as a way of shifting into the “Adaptive Cycle”, a cycle of asking for emotional support and creating secure social attachments, and away from the depressed state, in which individuals show subordination and remain insecurely attached, angry and withdrawn. This rationale is based on a similar conceptualisation of depression as an adaptive strategy, the Involuntary Defeat Strategy (IDS) (Sloman, 2000). However, most psychotherapy still focuses more on symptom reduction than the improvement of social processing (Silva, Cooper, Li, Lund & Patel, 2013).

To summarise, socio-evolutionary theories are increasingly conceptualising reduction of entropy as a unifying factor for understanding psychological processes (Badcock, 2012); more work is needed investigating the neural basis of discrepancies from self-concept and social prediction error specifically, as these should theoretically be key drivers of such processes. While the dACC/AI matrix does represent a strong candidate for processing of discrepancies, our findings suggest that future work might benefit from considering how its sensitivity is modulated by contextual information, for example by connectivity with emotional regulation or mentalising regions (Kawamichi et al., 2018).

Limitations of the Current Work

Any investigation of evolutionary principles is strengthened by demonstration of its relevance cross-culturally, therefore a key limitation of the current work is the use of a predominantly Western cultural sample. Individualist and collectivist cultures place differing emphasis on the importance of uniqueness and belongingness respectively (Marcus & Kitayama, 1991) which may influence perceptions of others and their behaviour (Han et al., 2013). This holds particular relevance when considering the importance of social norms, and cultural variations in the strength of their enforcement (Gelfand et al., 2011). Accordingly, cultural differences have been observed in response to cues of hierarchy and inclusion (Freeman et al., 2009), and in social cognitive processes including construal of self (Markus & Kitayama, 2010). Importantly, these differences may be evident at the neural level (Zhu, Zhang, Fan and Han, 2007; Ma et al., 2014). Cross-cultural validation of our findings, particularly regarding social norms, would be an interesting avenue for future research.

Additionally, the participant sample used in this protocol had an unusually high level of tertiary education, with 23.3% of the Depressed sample, and 14.5% of the Total sample, educated to doctoral level, as compared to just 1.4% in the UK general population at the time (OECD, 2019). Higher levels of education may have a protective effect on memory and cognition

(Crespo, 2014) and are associated with parental education level and socioeconomic background (OECD, 2019). Education level may therefore be a relevant factor when considering the applicability of these findings to the general population.

A potential issue in the design of the current study arises from the use of clinically homogenous testing groups. This design choice was made in order to test the hypotheses of Chapter 7, that when the interfering effects of Control participants were removed, Depressed-Only groups would behave more cooperatively than Control-Only groups. However, use of this design has possible confounding effects in the neuroeconomic games that followed, because the social experience of interacting within a Depressed group likely differs from that within a Control group. For example, Depressed participants may have observed more submissive behaviours in their groupmates than Controls, which might have influenced their beliefs regarding how much could be acceptably offered in the Ultimatum Game. While the statistical analyses employed in this thesis have mitigated this concern where possible, our interpretation of the data would be strengthened through replication of these tasks in mixed testing groups.

A potentially relevant limitation regarding the use of neuroeconomic games in this thesis are concerns about their ability to detect in-group bias. Stagnaro et al. (2017) found that group biases detected in a Prisoners' Dilemma Game were not subsequently detected in an Ultimatum Game (UG), concluding that participants' self-interested desire to make offers that would be accepted in the UG superseded group-level preferences. However, our study may have overcome this difficulty through the use of a group-induction; Goette, Huffman and Meier (2012) found that participants who experienced real social interactions with their group prior to an economic game showed stronger cooperation and altruistic norm enforcement compared to those assigned in-groups according to arbitrary labels. These findings suggest that future research utilising neuroeconomic games to examine social norms and in-group behaviour should prioritise including opportunities for social interaction if their findings are to be ecologically valid.

A final consideration regards the imaging methodology utilised in this thesis. Firstly, the data is presented with whole-brain measures first, before narrowing down to consider specific areas of interest. In hypothesis driven imaging work such as this, a potentially more informative method of presenting such data would be to begin with the results of ROI analyses, and focus on these before describing the findings of more exploratory whole-brain analyses. Future published work will present the findings described here in this alternative format. Secondly, it is useful to note the limitations inherent in fMRI and in the subtraction methods utilised here. Such subtraction-based designs have been criticized for their reliance on "pure insertion", the idea that you can swap out a discreet component of a cognitive task, and emphasise the importance of characterizing regionally specific interactions to overcome this issue (Friston et al., 1996). More broadly, fMRI is limited by its reliance on a surrogate measure, blood oxygen level, to infer the activity of neurons. This approach struggles to differentiate function-specific activity and neuromodulation, and is vulnerable to influence by the sparsity of neurons in the cortical region involved (Logothetis, 2008).

9.5. SUMMARY

Major Depressive Disorder (MDD) is one of the most prevalent health conditions in the world (Global Burden of Disease Study, 2017) and is linked with disruption to education, relationships, and employment (Kessler, 2011). The work reported in this thesis aimed to expand our understanding of social processing in depression, by clarifying the role of neural regions typically associated with pain and conflict under social conditions, and addressing the previously under-researched domains of social risk and self-discrepancy. Biases in social processing in depression were explored within a socio-evolutionary framework, with particular reference to the Social Risk Hypothesis of Depressed Mood (Allen & Badcock, 2003). The thesis presented neural and behavioural evidence that depression is associated with increased sensitivity to an exclusion-relevant context (in-group interactions) and stronger enforcement of social norms (Chapters 6 and 7) alongside reduced social risk taking (Chapter 8). This thesis also discussed the relevance of discrepancy to theories of affect as a socially homeostatic mechanism, presenting neural evidence of a negative processing bias for such discrepancies in depression, linked to activation in the dACC/AI matrix (Chapters 4 and 5) and suggesting a role for perfectionism as a transdiagnostic sensitivity to such discrepancies. Socio-evolutionary frameworks provide a unique perspective for understanding affective disorders, with some ‘deficits’ usefully reconceptualised as adaptive mechanisms. Future research should utilise neuroeconomic games to further investigate these frameworks, particularly in relation to assessing social function as a transdiagnostic marker, and to better characterise the impact of contextual and relational social factors in clinical depression.

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APPENDICES

Appendix 1 (Chapter 1)

Appendix 1.1. DSM-5 Criteria for Major Depressive Disorder

Major Depressive Disorder In children and adolescents, mood can be irritable.
5 or more of 9 symptoms (including at least 1 of depressed mood and loss of interest or pleasure) in the same 2-week period; each of these symptoms represents a change from previous functioning • Depressed mood (subjective or observed) • Loss or interest or pleasure • Change in weight or appetite • Insomnia or Hypersomnia • Psychomotor retardation or agitation (observed) • Loss of energy or fatigue • Worthlessness or guilt • Impaired concentration or indecisiveness • Thoughts of death or suicidal ideation or suicide attempt
Persistent Depressive Disorder In children and adolescents, mood can be irritable and duration must be 1 year or longer.
Depressed mood for most of the day, for more days than not, for 2 years or longer. Presence of 2 or more of the following during the same period and never without symptoms for more than 2 months. • Poor appetite or overeating • Insomnia or Hypersomnia • Low energy or fatigue • Low self-esteem • Impaired concentration or indecisiveness • Hopelessness

Appendix 3 (Chapter 3)

Appendix 3.1: Social Values Questionnaire (Griffiths et al., *in Prep*)

Social Values Questionnaire

Instructions: Below you will find a list of personal characteristics (ways to describe people) that we can think of as having 'social value'. By social value we mean the extent to which these characteristics are ones that you would appreciate and consider important either in yourself, or in other individuals within your social group.

We know that people vary in what characteristics they think are socially valuable. In this measure we want to find out what *you* think of as socially valuable in your social world. It is your own opinions that we want to know about. It is also important to note that we want to understand what you *think* is valuable. This is not a measure of how strongly you would actually rate yourself or your social contacts on these characteristics.

Please, go through the items below and tick ***how valuable you think each characteristic is in your social world***. Please be honest with your answers!

Item How socially valuable is being…	Not valuable at all	Not valuable	Hardly valuable	Neither	Somewhat valuable	Valuable	Highly valuable
Affiliation/Intimacy							
Kind							
Playful							
Sympathetic							
Nurturing							
Mindful							
Agreeable							
Welcoming							
Cheerful							
Close							
Warm							
Likeable							
Loving							
Friendly							
Utility/Usefulness							
Generous							
Helpful							
Wealthy							
Responsible							
Trustworthy							

Reliable							
Protective							
Polite							
Unselfish							
Sharing							
Emotionally supportive							
Practically supportive							
Loyal							
Compassionate							
Caring							
Sincere							
A team player							
Law-abiding							
Passive							
A problem-solver							
A hard worker							
Advocacy/ Agency							
Independent							
Opinionated							
Influential							
Political							
Serious							
Defensive							
Impressionable							
Peaceful							
Determined							
Faithful							
Argumentative							
Respectful							
Stable							
Judgemental							
Wholesome							
Open-minded							
Co-operative							
Honest							
Identity/Individualism							
Unique							
The owner of the latest gadgets							
Fun							
Quirky							
Authentic							
Fashionable							
Religious							
Clean							
Outgoing							

Quiet							
Vain							
Open							
Conscientious							
Creative							
Silly							
Charismatic							
Attractive							
Popular							
Expressive							
Humble							
Informative/ Intelligent							
Wise							
Knowledgeable							
On top of all the gossip							
Intelligent							
Cultured							
Artistic							
Educated							
A storyteller							
Organised							
A high-achiever							
Talented							
Technological							
Organised							
Skilful							
Conversation							
Engaging							
Relaxed							
A gossip							
Funny							
Witty							
Entertaining							
A conversation starter							
Talkative							
Sociable							
Boastful							
Antisocial							
Hostile							
Rude							
Unpredictable							
Excluding							
Aggressive							
A bully							
Selfish							
Negative							

Neglectful							
Mocking							
Someone who embarrasses others							
Someone who interrupts							
Insulting							
Ignorant							
Moody							
Jealous							
Spiteful							
Rebellious							
Unstable							
Stubborn							
Closed-minded							
Dominant							
Tough							
Competitive							
A dictator							
Confident							
Strong-minded							
Bossy							
Controlling							
Powerful							
A fighter							
An alpha							
Brave							
Intimidating							
Arrogant							
Superior							
Bold							
A risk-taker							
High in self-esteem							
Pushy							
Social media/ technology							
Computer-literate							
A cyberbully							
Being computer-savvy							
An online troll							
An online blogger							
Popular online (large number of friends/ followers)							
An online gamer							
Opinionated online							

Appendix 3.2: Testing guidelines and adverse events protocol

This is the guidelines followed for general testing procedures at the MRC Cognition and Brain Sciences Unit, Cambridge.

A formal risk assessment should be made prior to testing. A checklist on the next page is provided to assist in the assessment.

Lower risk studies will include those in which:

- healthy volunteers are recruited or volunteers who are deemed fit by the research team to take part in the study without undue distress being caused to participant or tester.
- neutral stimuli are used (e.g. normal range of cue words not all pleasant or unpleasant and none that under normal circumstances would be expected to produce an adverse reaction).

Higher risk studies will include those in which:

- participants are selected because they belong to a potentially vulnerable group (i.e. depressed/ anxious)
- inductions are used with the intention of inducing a potentially vulnerable state (e.g. negative mood induction)
- emotional stimuli are used (e.g. unpleasant IAPS pictures)
- researchers have consistently found that on previous occasions volunteers have become distressed with the tasks.

Special consideration: Inexperienced testers, new graduate students and new placement students should not be asked to run higher risk studies (or studies which could potentially fall into the high-risk category) without adequate training and support.

Training and support: It is the responsibility of supervisors or line managers to ensure that all research staff are fully competent in carrying out the tests and that strategies for dealing with potential problems have been outlined prior to testing.

'Buddy' system: New testers will be assigned a junior member of the cognition and emotion research team to act as a 'buddy'. The aim of the buddy system is to provide extra advice and support.

Contingency plan: If a proposed study falls into the high risk category, and panel members will be involved in the research, a brief contingency plan should be submitted to the panel office at the time the request is made for volunteers. The plan should provide details of what action will be taken to reduce the risk of distress to volunteers and to testers. The contingency plan must be agreed by the researcher and line manager or supervisor and signed by both parties.

Please note:

- All new members of the research group must find out from their supervisor/line manager if the research that they will be conducting is already covered by an existing ethics application.
- If their research is covered by an existing ethics application, then they must read the application and send a letter to the ethics committee stating that they agree to comply with all aspects of the application.
- If the study is not covered by an existing ethics application, then an application must be made under the guidance of the supervisor/line manager.

Risk management checklist

- ❑ Will the experiment use stimuli that could elicit a strong emotional reaction? (e.g. unpleasant IAPS pictures)
- ❑ Will the experiment use a negative mood induction?
- ❑ Will the experiment use any invasive techniques? (e.g. electrophysiology)
- ❑ Will potentially vulnerable (e.g. anxious or depressed) volunteers be asked to take part in tasks that might increase their vulnerable state?

If the answer to any of the items above is yes, you are required to send a letter to all potential volunteers explaining the nature of the experiment. The letter must be sent prior to recruiting volunteers over the telephone.

Pre-test:

- ❑ If you believe that your study might cause undue distress, and your volunteers intend to drive to the unit to take part, you should ask if they would prefer to be collected prior to the study and taken home afterwards in the unit car.
- ❑ In the event of participants becoming distressed as a result of taking part in the research, what plan of action do you intend to take?
- ❑ If a clinical psychologist might be needed to provide back-up support (e.g. following an adverse reaction to a negative autobiographical mood induction), which clinician has agreed to act on your behalf?
- ❑ Have research-relevant assessments been made to check participants' suitability to take part? (e.g. mood check, claustrophobia check)
- ❑ If the study involves repeated use of keyboard or mouse, have any checks been made concerning repetitive strain injury or arthritis?
- ❑ If there is a possibility that participants may become upset during the test, have you got a box of tissues with you in the testing room?

Post-test:

- ❑ Has the nature of the experiment been fully explained and was the participant given the opportunity to have any questions answered.
- ❑ What was the participant's reaction to the experiment? Was there anything about the experiment that they did not like? Will participants be given a feedback sheet to allow them to comment on their experience of taking part in the study?
- ❑ Is the participant's mood at its normal pre-testing level?
- ❑ Are you giving participants an information sheet with a contact telephone number of the researcher on it to take away with? For previous studies using mood induction procedures, contact sheets have included the following wording: *"We always try to ensure that when people leave the experiment, their mood has returned to normal. On rare occasions, people can find that their mood drops again after they have returned home. We do not expect this to happen but it is possible. If your low mood returns and you feel that your distress is due to the mood induction then call us on the telephone number below and we can discuss how best to help you."*

What to do if participants become distressed as a result of taking part in the research:

- Sit and listen, and offer the participant a drink of tea or coffee.
- If necessary offer a confidential talk with a clinical psychologist.
- If the participant is unable to drive home, the unit policy is to drive the person home yourself in the unit car (you must see Anthea to complete the necessary forms). If this is not possible ask Jackie Harper or Pete Williams if they are willing to drive you and your volunteer to the participant's home. If all else fails, take the participant home in a taxi.
- Ask if the participant would mind if you called them later that day/the next day to check that they are OK.

Research using mood inductions, unpleasant IAPS pictures, invasive techniques and training in cognitive bias

The following guidelines have been adapted from the CBU policy on the use of mood inductions:

- Any researcher proposing to carry out research involving mood inductions, unpleasant IAPS pictures, invasive techniques or training in cognitive bias should send an email/letter to the Director prior to testing to obtain consent.
- A covering letter must be sent to prospective volunteers indicating the nature of the research they are being invited to take part in
- A contingency plan must be submitted to the panel office describing what measures will be taken to reduce the risk of distress to volunteers and to testers, and what action will be taken if an individual does suffer as a result of the testing (see description in ethics application question 10).
- Volunteers must sign a written consent form before beginning the experiment.
- If on the day of testing, the participant has changed their mind since agreeing to take part in the study and no longer wants to engage in the mood induction/view the IAPS pictures/be wired to the equipment, an alternative task must be made available for them to complete.
- Volunteers must be reminded that they are free to terminate the experiment at any point.
- Experimenters must ensure that volunteers' mood has returned to 'normal' (pre-testing level) before concluding the experimental session.
- Volunteers should not be asked to take part in other tests immediately following the experiment.
- A clinical psychologist should be approached and asked whether they would be prepared to talk to any participants who suffer an adverse reaction as a result of the experiment. This is not expected to happen but provision should be made in case it does occur. The discussion would take place at a time mutually convenient to the clinician and the volunteer.

Additional recommendations

- Scientists who are not clinically trained, but who wish to do mood induction research, must obtain guidance from someone experienced in the use of this technique. Guidance should cover screening of volunteers, implementation of the procedure and (most important of all) how to assess whether volunteers have returned to normal mood at the end of the experiment.
- The mood-state of volunteers must be screened before experiments using depression induction procedures, unpleasant IAPS pictures, invasive techniques or training in cognitive bias. Great care must be taken when testing volunteers scoring 14 or more on the Beck Depression Inventory, scoring above 8 on the HADS, and scoring 45 or more on the Spielberger Trait Anxiety Questionnaire. Only testers with suitable training should test volunteers with high depression or anxiety scores.
- As autobiographical mood inductions are more likely to lead to longer-term distress once the participant has returned home (compared with musical or film inductions) a negative autobiographical induction should not be used unless it forms an essential aspect of the study.
- Group mood induction should not take place unless a special case is made for it to the Ethical Committee.

Potential problems and advice on what to do

Participant care

Example 1: If a participant becomes distressed during the study….

If during an experiment (e.g. a study using an autobiographical memory task) a participant becomes distressed and begins to cry, testing should be curtailed. Sit tight, listen and make sympathetic noises if appropriate. Try to give the impression that their emotion is absolutely justified, they are normal, and you care that they are currently distressed. Give them time to recover. If it feels 'unfinished',

ring the participant the next day to check they are OK. Provide feedback to the panel about the incident.

Example 2: If the participant's mood has not returned to normal after testing….

If after an experiment (e.g. a study using a negative mood induction) a participant's mood has not returned to pre-testing levels, explain that it is not unit policy to send participant's away from an experiment feeling unhappy. Take them to a quiet room, if possible, play them relaxing music/ a tape of mood enhancing sounds, offer them a drink, and allow them to sit and relax for a while. Give the participant an information sheet with a daytime contact number (see page 2). Should the participant's low mood return and they attribute it directly to the study, they can then telephone and discuss their feelings with the researcher. Provide feedback to the panel about the incident.

Example 3: If a participant reports feeling adverse effects a week or more after testing….

If, after taking part in a high-risk study (e.g. research using unpleasant IAPS pictures), a participant reports having intrusive thoughts about the stimuli they were presented with, listen to the individual's concerns, and talk to them about their experience. If they remain unhappy, invite them to discuss their concerns with the nominated clinician. Provide feedback to the panel about the incident. Follow-up the complaint 2-3 weeks later with a telephone call to see how the participant is feeling.

Example 4: If a participant faints or becomes ill during testing….

Before you begin testing, check which members of staff are first aid qualified, which are situated nearest to your testing space and whether they are willing to be called upon should the need arise. If a volunteer does become ill during testing let the panel managers know about the incident. Follow-up with a telephone call the next day to see how the participant is feeling.

Researcher support

Example 1: Dealing with distressed participants…

If the researcher suspects that a participant is becoming unduly distressed by the experiment, then testing should be curtailed. After measures have been taken to deal with the participant's distress (see above), the tester should discuss the incident with their line manager or supervisor. This debriefing for the tester should aim to provide reassurance and advice about the way the incident was handled, as well as advice on what further action should be taken.

Example 2: If repetitive testing leads to tester-distress….If repeated testing using emotional stimuli (e.g. unpleasant IAPS) causes distress for the tester, or an incident with a participant has created 'emotional wear-and-tear', the tester should seek out their 'buddy' or their line manager/supervisor to discuss the problem. This debriefing for the tester should aim to provide reassurance and advice. If it is the material that is causing particular problems, the issue should be raised with the line manager. They should discuss ways in which to alleviate distress to the tester (e.g. by waiting outside the room during critical parts of the experiment) and if necessary, revise the experiment. The tester should be given as much time and emotional support as they require. Testing should only continue when the tester feels confident to do so.

Example 3: Working outside normal hours or working alone outside the unit….

Junior staff/ students should avoid working alone outside the unit, if possible. All staff testing outside the unit should register their whereabouts, contact details and expected return time with their line manager, their 'buddy' or with reception staff before they leave. They should take a unit mobile phone and inform their line manager/'buddy'/reception when they return. Junior staff/ students should also avoid testing participants in the unit outside normal working hours. If testing outside office hours proves essential, arrangements should be made to make sure that an experienced member of the group is present in the building, who can provide assistance should it be needed. All staff working out of hours should sign in to register their presence.

Appendix 3.3: MRI Adverse Events Protocol

Abnormal (Incidental) Findings

The Cognition and Brain Sciences Unit is a cognitive neuroscience research unit and does not provide any diagnostic services. This policy will be clearly stated on the volunteer information sheet.

However, in order to ensure that only participants with appropriately healthy brains are included in our studies, and also to pick up any major abnormalities that do occur, structural T2-weighted scans will be run on all participants if not already run within 2 years. Even though we do not provide a diagnostic service, a Radiologist reviews all structural T2-weighted scans (taking into account their demographic details, e.g., age). In the event that a significant abnormality is noticed by the Qualified MRI Operator, this will be brought to the attention of the CBSU Medical Monitor, who is responsible for acting on this information. It may be necessary to exclude such participants from the study in which case the reasons for the exclusion will not be fed back to the researcher. The Medical Monitor will take responsibility for referring the individual concerned for further clinical evaluation where this is appropriate. Note that, if a volunteer later contacts a researcher to ask about possible abnormal findings, the researcher should only take their contact details, and then tell the Medical Monitor and Radiographers, one of whom will contact the volunteer. A researcher should not try to give any other feedback to the volunteer.

Appendix 3.4: CBU Adult Volunteer Panel Study Consent Form

Study Title: The influence of mood on social rank, social risk-taking and decision-making
Principal Investigator: Dr Tim Dalgleish
Researcher(s): Kirsty Griffiths; Dr Jason Stretton; Daisy Follett
CPREC/NRES Code: PRE.2017.083

Agreement to continued membership of the CBU Adult Volunteer Panel

The MRC Cognition and Brain Sciences Unit (CBU) is part of the University of Cambridge (from July 1st 2017). The University of Cambridge have the responsibility for safeguarding research data and personal information.

Please initial to indicate that you have read and each point

1. I agree to my continued membership of the CBU Adult Volunteer Panel and understand that this means the University of Cambridge holding my personally identifiable information (e.g. my name and address) that I provided when I registered as a volunteer with the MRC Cognition and Brain Sciences Unit Adult Volunteer Panel. This includes information given before the CBU became part of the University of Cambridge.

2. I understand that the CBU Volunteer Panel uses a commercial web interface (sona-systems.com) to communicate with volunteers and that, whilst I remain a member of the Panel, my personal information is therefore held on computer servers belonging to this company in Canada and the Netherlands. These are compliant with EU law on data protection. I agree to this. ____

3. I understand that, should I no longer wish to be a member of the Panel, or I cannot be contacted ____
5 years after my last participation, all personally identifiable information held about me will be deleted from the Panel and the Sona-systems website.

4. I confirm that I have had an opportunity to read the CBU Adult Volunteer Panel Information sheet and the CBU Human Subject Privacy Policy, had the opportunity to consider this information, ask any questions and had these questions answered satisfactorily. ____

Agreement to participate in this study:

5. I confirm that the nature of the above named study has been explained to me and that I have agreed to take part. ____

6. I confirm that I have read the participant information sheet for the above study. I have had the opportunity to consider the information, ask questions and have had these answered satisfactorily. ____

7. I understand that my participation in the above study is voluntary and that I am free to withdraw at any time without giving a reason. ____

8. I understand that my personally identifiable information, such as my name, address and date of birth are treated as highly confidential by the research team and kept in a secure computing area and/or in a locked filing cabinet. I have read and understood for how long these details will be kept by the researchers running this study. ____

9. [IF RELEVANT] I understand that MRI radiographers will complete a safety screening sheet that will include my name, address and date of birth. I understand that this is retained by the radiographers separately from my research data for 10 years in case of safety audit. I agree to this. ____

10. [IF RELEVANT] I understand that the CBU has a duty of care to volunteers and the general public that, in exceptional circumstances, places limits on its duty of confidentiality to research participants. I understand and agree to this. ____

11. I agree that my *anonymised* research data from this study will be kept in the long-term, may be combined with data from other CBU studies to answer new research questions,

may be shared with other researchers or may be made 'Open' without new consent being sought from me. ____

12. I agree to the CBU panel manager receiving the scores from measures I have completed in this study and making these available to other researchers within the CBU for the purposes of inviting particular participants (e.g. fluent French speakers) to take part in specific studies. ____

To indicate your agreement with points 1-12 above, please sign below

Panel id: Name of Participant:

Signature: …… Date: ……

Appendix 3.5. Participant Information Sheet

Adult Volunteer Panel Study Participant Information Sheet

Principal Investigator: Kirsty Griffiths; Daisy Follett
Researcher(s): Dr Tim Dalgleish; Dr Jason Stretton
Study Title: The influence of mood on social rank, social risk-taking and social decision-making
CPREC/NRES Code: PRE.2017.083

You are being invited to take part in a research study. Before you decide whether or not to participate it is important that you understand why the research is being done, what it will involve and how the information collected from you is stored and used. Please take time to read the following information carefully and discuss it with others if you wish. Ask us if there is anything that is not clear or if you would like more information. Take time to decide whether or not you wish to take part.

What is the purpose of the study?

The aim of this project is to investigate how information pertaining to relationships and socially risky scenarios are processed at a behavioural level in people with varying mood.

Who is organising and sponsoring this research?

The study is organised by Kirsty Griffiths/Daisy Follett and is sponsored by the University of Cambridge, this means that the University of Cambridge takes responsibility for the study.

Has the study been approved?

This study has been reviewed and approved by an independent group of people, the Cambridge Psychology Research Ethics Committee, who have a duty to protect research volunteers' safety, rights, wellbeing and dignity.

Why have I been invited to take part?

You have been asked to participate either because you responded to an advertisement or because you previously volunteered to be a member of the Volunteer Panel at the Cognition & Brain Sciences Unit.

Do I have to take part?

It is up to you whether or not to take part. Before deciding you should read this information sheet and ask about anything that is not clear. If you decide to take part we will ask you to sign a form indicating that you have agreed (consent form). However, even after you have signed that form you can withdraw from the study without having to give us a reason.

You should be aware, however, that we aim to anonymise our results (separate and remove your personally identifying information) as soon as possible after data collection to protect your privacy. If you decide to withdraw sometime after your participation it may therefore not be possible to identify and remove your specific results.

What will I be asked to do in the study?

Taking part requires you to visit the MRC Cognition & Brain Sciences Unit for a session of up to 2 hours. You will be asked to do one or more computerised tasks that test your perception and processing of relationships and social risk. The tasks you will be invited to do will look at how we perceive and process the relationship and risk of others. For example, you may have to recall a

diagram that may reflect the relationship of others around you. In another example you might be given a hypothetical (socially risky) scenario and you will need to decide on one of two options for overcoming the problem. All of the tasks will be explained in detail before you start and we will answer any questions you may have. These tasks are not a test of your abilities but instead a measure for us to see how people in general perceive the world. Sometimes there is no 'correct' answer, we just want to know what you can see and memorise.

In addition to the above, you will be asked to complete a set of questionnaires regarding your mood and self-perceived social rank. The answers you provide in the questionnaires are at complete disclosure to the researcher.

Will video or audio recordings be made?

This study does not involve video or audio recording.

Will I be paid for taking part or have my expenses paid?

To thank you for your contribution to this study we give you £6 for each hour of your time, and reimburse your travel expenses, up to a limit that you can discuss with the researcher. You may take part in a task which provides the opportunity to win additional compensation, if this is the case it will be made clear to you prior to the task.

What is an MRI scan?

MRI stands for "magnetic resonance imaging." MRI uses a strong magnetic field to give us a 3D picture of your brain and allows us to see changes in the activity of different parts of your brain as you do tasks. MRI is a non-invasive technique (all the scanning equipment is outside of the body) that is used routinely in modern medicine. It has no known side effects. It does not involve injections or x-rays. Because of the strong magnetic field a qualified MRI operator will ask you to remove all metal belongings (which we will store safely) and check that you have no metal within your body. You remain clothed throughout and metal that is part of your clothes (jeans rivets etc.) is normally unproblematic. If the operator does not think it is safe we will not continue. They will also ask you questions to ensure that you will be comfortable in the scanner. If you are very uncomfortable in small, confined spaces you may not wish to participate. If it is safe and you are happy to proceed, during the session you will lie comfortably on a hospital-style bed with your head inside the MRI scanner whilst the scans are taken.

It is a bit noisy and you will be asked to wear ear-plugs. You will be provided with a hand-held alarm that you can squeeze if you become uncomfortable or distressed at any time. This will alert the operator who will remove you from the scanner immediately. To collect good information it is important that you keep your head as still as possible when in the scanner. Scans typically last 30 to 60 minutes.

What if the MRI scan suggests something unusual about my brain?

We do not run diagnostic scans, but if something abnormal is detected (that was not already on your records), you will be appropriately counselled and referred to an appropriate specialist in consultation with your GP, if that is what you would like. There can be benefits of detecting problems in terms of starting treatment earlier than would otherwise be the case but, very occasionally, findings may have implications for future employment and insurance.

What are the possible risks/side effects of taking part?

There are no obvious risks from the computer tasks that you will complete. If you become tired or uncomfortable during any of the tasks, please let us know and we will take a break or end the

session. Remember you can withdraw from the study at any time without needing to give us a reason. With the appropriate safety checks in place MRI, MEG and EEG are safe, non-invasive imaging techniques, with no known side effects.

What happens to my personally identifiable information?

You have provided us with two types of information. Personally identifiable information includes your name, address and date of birth – information from which you could be identified and that we use to contact you, calculate your age and so on. Anonymised research data includes information like the buttons you pushed on a computer task, information from a brain scan and your answers on a questionnaire; in other words, once it is no longer connected to your Personally Identifiable Information, information from which it would not be possible, or would be very difficult, to identify you personally.

We separate your Personally Identifiable Information from your Anonymised Research Data and treat these two types of information very differently.

The University of Cambridge Data Protection Officer is the Data Controller for any Personally Identifiable Information that you have given us. Contact details: The Old Schools, Trinity Lane, Cambridge CB2 1TN (address removed).

Electronic Personally Identifiable Information is either entered directly into a secure area of our computer system or transferred there as soon as possible after collection. Personally Identifiable Information on paper records is kept in a locked filing cabinet within a secured building. Personally identifiable information is treated with strict confidentiality and in line with Data Protection Act 1998, which regulates the collection, storage, processing and disclosure of such information. This information is held very securely and only for as long as is necessary (e.g. for contacting you and for the management of the research

If you have questions about how long and for what reasons your Personally Identifiable Information is held, please ask the researcher.

As this is a brain scanning study, the scanner operator will go through a safety-screening sheet with you. This is an important record that safety procedures were followed. This sheet includes your name, address and date of birth and the name and address of your General Practitioner (GP). The scanner operators keep a secure copy of this sheet for 10 years in case of safety audit, even if you stop participating in studies here. After 10 years this record will be deleted.

What happens to my anonymised research data?

Your anonymised research data, typically combined with similar information from other volunteers, will be used for scientific research. The results are presented in scientific papers and talks, in teaching and in explaining our science to health professionals, school groups and the public in general. We take great care to ensure that individuals cannot be identified from our research outputs.

Undertaking scientific studies is expensive and relies on the generous contribution of time from volunteers. To make the most of your anonymised research data we plan to look after it for the long term and may use it to answer research questions beyond those for which it was originally collected. This may include combining anonymised research data from this study with anonymised data from other studies in the CBU in which you have been involved (e.g. brain scanning studies) and with the anonymised answers that you gave when you joined the Panel. In addition to our own analyses, we agree with the principle that research data, often collected with public money, are a public good, produced in the public interest, which should be made openly available with as few restrictions as

possible in a timely and responsible manner. Many of the bodies that fund our research insist that we follow this principle. In line with this we may also share anonymised research data with other researchers in the UK and around the world and may make anonymised research data available as "Open Data". Open data can be downloaded free of charge by anyone interested in the research or who wishes to repeat or conduct new analyses. This allows others to check our results and helps avoid research duplication. If research data is made Open we have no control over how that information is used.

We are very aware that, sometimes, anonymised research data could be used to identify an individual (for example, questionnaire responses about life events could identify a particular person to someone who knows him or her or who had read a newspaper story of similar events). In such cases we take great care to reduce the chances of this individual being identified by omitting critical details or not sharing even anonymised data with anyone outside of the original research team.

Can I get access to my results from the study?

It is important that, as researchers, we minimise potential harm to volunteers in our studies. We often use new techniques and interpreting research data can be complicated and has the potential to cause undue concern. For this reason we do not divulge individual results (with the exception of abnormalities detected on MRI scans, see above). If you have concerns about your performance please discuss these with the researcher.

If you are interested in receiving the general results of the study upon completion via email, please let the researcher know.

Are there compensation arrangements if something goes wrong?

The study has insurance to deal with any claim in the very unlikely event of anything going wrong that causes harm.

What should I do if I have a complaint about the study?

We are keen that volunteers feel informed and well treated when they take part in our research. If you have a complaint about this study please contact the Principle Investigator listed at the end of this information sheet in the first instance. If you are not happy with the response, please contact the Director of the Cognition and Brain Sciences Unit (director@mrc-cbu.cam.ac.uk). Further steps can be taken through the University of Cambridge if necessary.

Thank you for considering taking part in this study. Our research depends entirely on the goodwill of potential volunteers such as you. If you require any further information, we will be pleased to help you in any way we can.

Further information and contact details

Daisy Follett

MRC Cognition & Brain Sciences Unit

15 Chaucer Road, Cambridge. CB2 7EF

Appendix 3.6: Written Debriefing Form

Principal Investigator: Dr Tim Dalgleish
Researcher(s): Kirsty Griffiths; Dr Jason Stretton; Daisy Follett
CPREC/NRES Code: PRE.2017.083

Thank-you for your participation, you have completed the study.

The purpose of this research is to determine whether information related to social rank and social risk are processed at a behavioural and neural level in people with varying mood. It has been demonstrated that individuals with low mood tend to perceive themselves as inferior to others and exhibit submissive behaviour in social interactions and consequently minimizing their social risks. Whilst we know depression is theorised as the inability to terminate these behaviours, there has been little research investigating the cognitive mechanisms involved in processing social rank in adolescents, nor their relationships to the risk of developing depression or other mental health conditions, using experimental tasks. This study aims to use behavioural and neuroimaging measures to investigate the perception of social rank and social risk processing in adolescents and adults.

In this study we may have presented you with an ambiguous picture or scenarios that could be perceived as a social hierarchy or something that is considered socially risky. These may be experimentally manipulated, such as your social rank, to observe behavioural changes within the experimental task. This information may have been withheld from you as it is necessary for the purposes and conduct of this research. If you have any questions about the nature of manipulating social rank, please contact Kirsty Griffiths (address removed) or Daisy Follett (address removed).

In addition to the above, you may have been asked to complete a range of questionnaires regarding your mental health. These are part of standard procedures in studies within the Emotion group and all information will remain confidential. Sometimes people find the subject matter of these questionnaires alarming. If answering any of these questions led you to feel distressed and you would like to speak to someone about your thoughts, please contact our trained clinical psychologist Dr Caitlin Hitchcock on (address removed) or call (number removed). If you feel at risk of self-harm, for immediate support you can contact the First Response Service. Call 111 and select option 2.

If you have any complaints, concerns, or questions about this research, please feel free to contact Kirsty Griffiths (address removed) or Daisy Follett (address removed). This can include your right to withdraw (leave) from the study, where your data will be removed with no questions asked. This study has been granted clearance according to the recommended principles of Cambridge Psychology Research Ethics Committee (CPREC) guidelines, and University of Cambridge's polices.

Finally, thank-you again for helping us with our research.

Kirsty Griffiths & Daisy Follett

Appendix 3.7: Cambridge Psychology Research Ethics Committee Application Form

UNIVERSITY OF CAMBRIDGE

COUNCIL OF THE SCHOOL OF THE BIOLOGICAL SCIENCES
Cambridge Psychology Research Ethics Committee

Question 1: Title of the study

The influence of mood on social rank, social risk-taking and social decision-making

Question 2: Primary applicant

Dr Tim Dalgleish (TD), BA, MA, PhD, MSc, Clinical Psychologist and Cognition & Mental Health Programme Leader, Medical Research Council Cognition & Brain Sciences Unit

Question 3: Co-applicants

Kirsty Griffiths (KG), PhD Candidate, Medical Research Council Cognition & Brain Sciences Unit.

Daisy Follett (DF), PhD Candidate, Medical Research Council Cognition & Brain Sciences Unit

Jason Stretton (JS), Investigator Scientist, Medical Research Council Cognition & Brain Sciences Unit

Question 4: Corresponding applicant

KG (address removed)

Question 5: In which Department(s) or Research Unit(s) will the study take place?

Data recordings, analyses and storage will take place at:
Medical Research Council, Cognition and Brain Sciences Unit, 15 Chaucer Road, Cambridge, CB2 7EF.

Question 6: What are the start and end dates of the study?

October 2017 to June 2022 (exact study length will depend on recruitment).

Question 7: Briefly describe the purpose and rationale of the research

The aim of this project is to investigate how information pertaining to social rank and social risk are processed at a behavioural and neural level in people with varying low mood. Individuals with low mood tend to perceive themselves as inferior to others and exhibit submissive behaviour in social interactions and consequently minimizing their social risks.

Social rank refers to an individual's social standing in a group, either as dominant or subordinate. Social rank theory argues low mood is associated with the evolutionarily defined behavioural response to failure of upward rank challenges and acceptance of downward authority. These behaviours are known asinvoluntary defeat strategies and serve to signal the end of the rank challenge, transferring benefit to the survival of the group in the maintenance of social rank order. Depression is theorised as the inability to terminate these defeat strategies, resulting in feelings of entrapment and hopelessness (Gilbert, 2000).

Research into the resilience of depression are now focusing their attention to adolescent development, where persistent low moods emerge. 50% of adults with psychiatric disorders experience their first onset at the age of 15, and 75% by age 24 (Kessler *et al.,* 2005). Of all mental health disorders that emerge during adolescence, depression is one with the largest impact on social and occupational functioning and reduced quality of life (Kessler *et al*., 2001). Reciprocal interactions between brain maturation and the social environment at this critical developmental stage may augment risk of mental illness or other health outcomes.

To our knowledge, there has been little research investigating the cognitive mechanisms involved in processing social rank in adolescents, nor their relationships to the risk of developing depression or other mental health conditions, using experimental tasks. This proposed study aims to use behavioural and neuroimaging measures to investigate the perception of social rank and social risk processing in adolescents and adults.

Question 8: Who is funding the costs of the study?

Medical Research Council
Cognition and Brain Sciences Unit
Cambridge
CB2 7EF
United Kingdom

Question 9: Describe the methods and procedures of the study

The research involves a series of experiments assessing the perception and processing of social rank and social risk. Some experiments involve presenting a series of stimuli that infer rank (i.e. visual pictures or auditory words or phrases), and then later testing the participant's ability to recall the information (see example Figure 1). In other studies, participants complete a range of social and economic decision-making tasks where there are probabilistic alternatives that are known to the individual. These studies are similar to what is described in existing neuroeconomic games, whereby social (hypothetical) scenarios of uncertainty will infer social risk (see examples in Figures 2 & 3). Behavioural responses (i.e. button presses, verbal recall or written information) and response time in some cases, will be recorded on a testing computer within the MRC Cognition & Brain Sciences Unit. In addition, some experiments may explore neural correlates via functional Magnetic Resonance Imaging (fMRI).

The experiments will vary in the number of standard psychological manipulations, such as stimulus type, attentional load, predictability etc., which are relevant to social theories that are under investigation. Social rank and social risk will be tested in several ways: sometimes directly via recall, selecting binary options to decisions or indirectly via reaction times to make a decision.

For some experiments, participants will have a photo taken of themselves which will later be used in the study. This is standard in tests of social rank and have been manipulated in previous studies TD and JS have applied in the past (e.g. PRE.2014.02). For these experiments, participants will be told in advance that the experiment is about the 'perception of social relationships' and that their photo will be taken

alongside confederates who have also completed the task. During some experiments, standardised assessments such as the Rey-Osterrieth complex figure test (ROCF) will be used to test baseline non-verbal memory. All participants will also complete a set of established questionnaires that have been empirically used in previous studies for testing social perception in individuals with varying mood at the MRC-CBU (for further details see **KG_Appendix1_Materials**). Participants will always be given a full debrief about the nature of the experiment in the end. Photos that have been taken will be destroyed once the experiment has been completed.

An experiment will typically last around 1 hour, with a maximum of 1.5 hours if necessary. Some experiments may require more than a single testing session. Participants will be allocated regular breaks throughout the experimental session. For behavioural experiments, participants will be seated in the testing cubicles within the MRC-CBU. These testing cubicles have been used for data collection for many years and have built-in cameras and alarms for the safety of the experimenter and participants. Future fMRI studies will apply the same study design as the behavioural studies, but will be presented in the Siemens 3T Prisma MRI scanner based at the MRC-CBU.

Participants will be provided with a general information sheet and detailed instructions about the tasks they will perform, before being asked if they would be willing to take part in the study and to complete a written consent form if so. All participants are free to withdraw from the study without giving any reason. For behavioural studies, participants will be told to read a Participant Information Sheet (PIS) detailing the nature of the study (see **KG_Appendix2.1_PIS_v2_Behavioural_adults)**. An adolescent version of the PIS form will be given to adolescents, which is comprehendible for younger individuals to understand (see **KG_Appendix2.1_PIS_v2_Behavioural_adolescents**). For neuroimaging experiments, additional information regarding MRI are available for adults (**KG_Appendix2.1_PIS_v2_MRI_adults**) and adolescents (**KG_Appendix2.1_PIS_v2_MRI_adolescents**). Consent forms will be signed and dated from the participant as proof of consent to the study, the adult (**KG_Appendix3.1_Consent_Adult**) and adolescent versions (**KG_Appendix3.2_Consent_Adoelscent**) are attached.

All participants will be screened for their suitability for fMRI using established questionnaires and guidelines adopted by the MRC CBU, detailed in the Standard Operating Procedures (SOPs), see **CBU_MRI_SOPS** enclosed. Participants will be continuously checked throughout the testing session and the experimenter will terminate the testing session if they exhibit discomfort.

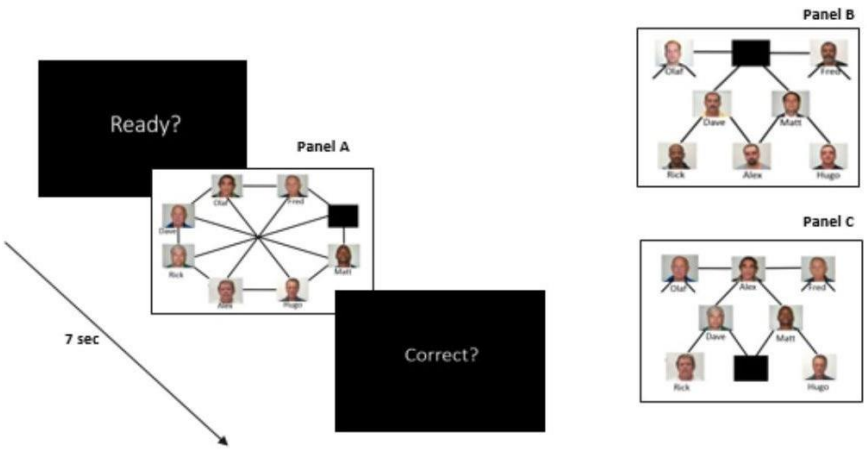


Figure 1. An example of a potential study where social rank is manipulated, adapted from Zitek & Tiedens (2012). Participants are shown either the equality diagram (Figure 1, Panel A), the hierarchy diagram where the participant is positioned as a high rank (Figure 1, Panel B), or the hierarchy diagram where the participant is positioned as low rank (Figure 1, Panel C). Black squares indicate where the participant's face will be positioned.

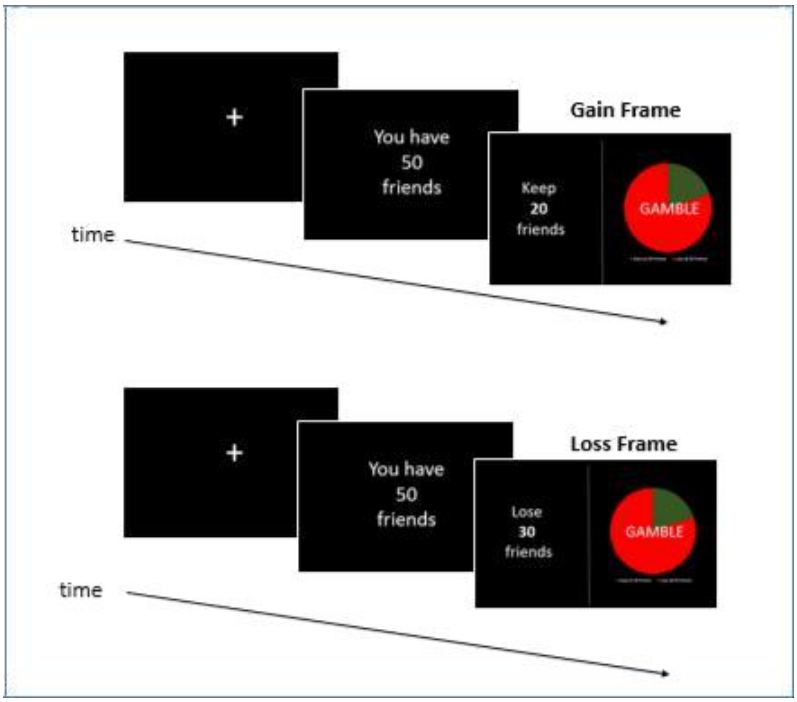


Figure 2. An example of a neuroeconomic game (framing effect), adapted from De Martino et al. 2006. Participants choose a binary option: a safe (risk-averse) or gamble (risk-prone) bet for social scenarios where the outcome is uncertain. The "gamble" option will be identical in both frames and will be presented as a pie chart depicting the probability of winning or losing. The dependant variable will be the number of times the individual selects the "gamble" or "safe" option in the Gain or Loss trials.

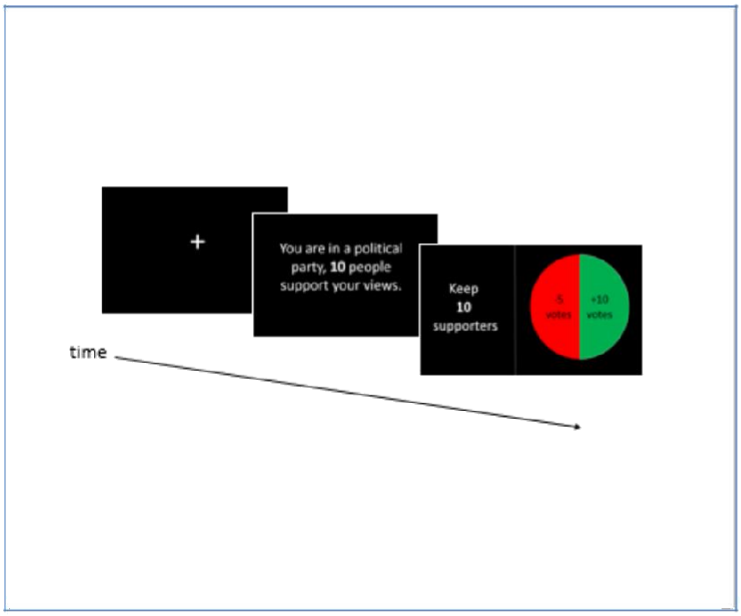


Figure 3. An example of a neuroeconomic game (loss aversion), adopted from Tom *et al.* (2007). Participants decide whether to accept or reject the mixed gambles that offer a 50/50 chance of either gaining or losing the offered amount. The size of potential gains/losses are manipulated independently, with gains from 10 to 40 supporters (2 vote increments) and losses ranging from 5 to 20 votes (increments of 1 vote). The dependant variable will be the response time to accept/reject the gamble and the number of gamble acceptances at each level of gain/loss.

Question 9a: Does the study involve any pharmaceutical or other compounds with physiological effects?

No.

Question 10: What ethical issues does this study raise and what measures have been taken to address them?

For behavioural experiments, there is little chance of discomfort. All auditory, visual stimuli will be presented within a comfortable setting. In some studies the experimenter may request a photo of the participant to add to the task. The photo will not be linked to the identification of the participant and will be deleted once the task is finished. Some of the stimuli may be emotional salient that some participants with variable mood may be sensitive to. In the unlikely case where a participant may become distressed, we have a protocol in place in order to ensure their wellbeing. A full description of our protocol is included in **KG_Appendix4_Protocol** but in summary, in case of distress we follow these steps -

1. Provide a safe space

Participants are offered a drink and a peaceful environment in which to relax, to allow any adverse effects to dissipate. A member of the research team will remain with them for as long as needed.

2. Offer a confidential consultation with a Clinical Psychologist

If the participant remains upset or wishes to talk at length then they are offered the chance to speak with a nominated clinical psychologist, at a time that is mutually convenient. This will be followed up with a GP referral if necessary and/or contacting emergency services in case of crisis.

3. Ensure safe transport home and further follow up if necessary

The suitability of participants to drive is assessed, and alternative transport is arranged if necessary. Follow-up telephone calls are offered.
Full details about MRI are provided in the MRC CBU SOPs that are enclosed with this form. In summary, the fMRI scanner can be loud when it takes images, so the participants will be given headphones to block the sound. Also, the MRI scanner is confined which may cause some distress to a participant who is uncomfortable with small spaces and may not wish to participate. This information is conveyed to the participant when they are contacted to participate (see PIS), although it is expected that many volunteers will have previously participated in fMRI studies. MRI is a non-invasive imaging technique and there are no known side effects of participating in such studies. All MRI scans are checked by the radiologist and the procedures for dealing with incidental neurological findings are attached in MRI SOPs.

fMRI scanning and will be performed by professional radiographers or appropriately trained CBU staff. All proposed experiments will be presented and reviewed by the MRC CBU Emotion group and at the CBU's "Imagers Interest Group" (IIG). An application is then made to the CBU's Imaging Management Committee for approval, whereby additional checks about various aspects of the proposal will be reviewed by scientists working in a related research area.

Written informed consent will be obtained from each participant following explanation of the experimental procedures and methodology (see the PIS and Consent Form attached). The panel consent form will be used for behavioural experiments and neuroimaging studies. Participants will be asked to divulge personal information, including an update on their current mood and wellbeing, which may cause some distress and may lead to participant withdrawal. Participants will be ensured that all information will remain confidential, with all names replaced with digital ID numbers and secured in a database within the MRC-CBU. Participants and experimenters involved in these studies will be carefully monitored to ensure all procedures run smoothly without issue.

Question 11: Who will the participants be?

Adults (aged 18-65) are community volunteers with a self-reported history of low mood, selected from our MRC-CBU databases, similar to previous CPREC studies (e.g. PRE.2014.43; PRE.2014.02).

Adolescents (aged 11-16) will be recruited from the MYRIAD project, a separate research project that TD and KG are currently investigating (PRE.2015. 067). Adolescents with parental/guardian consent and have shown an interest in further research within the MRC-CBU will be contacted about studies available. An additional parental/guardian consent form, participant consent form and panel consent form will need to be signed before any studies are carried out. All information will be checked for language comprehension, and participants will be given an opportunity to ask any questions about the study.

A typical sample size of 40 participants (20 adults and 20 adolescents) for behavioural studies is an approximate number we anticipate on completing per study, with one study taking 2 years. For neuroimaging, we expect a similar sample size and running from 2020 onwards. This study recruitment will continue throughout the research period. All participants will be literate and fluent in English, with normal to corrected vision. Participants with current or previous treatment for current alcohol or substance abuse, current learning disabilities, or organic brain damage will be excluded from the study. For participants using fMRI, we will ensure that all participants are MRI-safe and suitable for testing. No participants will be directly recruited from the NHS.

Question 12: Describe the recruitment procedures for the study

Participants with varying degrees of low mood will be recruited from our long-standing volunteer panel This is our standard method of recruitment which has been previously approved by CPREC (e.g. 2005.25; 2010.11). Other members of the public interested in participating (in response to adverts for example) will be referred via the MRC CBU Volunteer Panel. All participants interested in studies addressing mood will be required to attend a screening session, where a clinical psychologist (or highly trained member of the Emotion Group) will collect information about their mood history. All information about a new volunteer member will be securely stored in an encrypted file within the MRC CBU, only restricted members of the Emotion group could access this.

Adolescents that wished to be contacted for future studies conducted at the MRC CBU will be recruited from the MYRIAD database. This was agreed by the Principal investigator of the MYRIAD project, TD.

In general, participants will be contacted by telephone, email or the MRC CBU online sign-up system to gauge their interest. The study will be explained to potential participants, and if they are interested in taking part they will be provided with the relevant information about the behavioural/neuroimaging study. If they agree to take part then testing sessions will be arranged. All personal information will be kept confidential and these provisions are in line with the MRC guidelines on Personal Information in Medical Research.

Question 13: Describe the procedures to obtain informed consent

Participants will be recruited from existing MRC Cognition and Brain Science Unit participant database, so all participants will have previously consented to take part in future research. Additional consent prior to the investigation (i.e. verbal consent over the phone or confirmed their attendance over email) and written consent will be collected at the time of the investigation. Written consent from a parent/guardian, in addition to written consent at the time of investigation, will be required for participants in the adolescent sample.

Participants will be emailed about the nature of the investigation and given the opportunity to ask any questions before taking part. If they agree to participate, written (signed) consent will be obtained using the enclosed MRC-CBU consent form for adults (**KG_Appendix3.1_Consent_Adult)** and adolescents **KG_Appendix3.2_Consent_Adolescent)**. Participants will be given time to decide on whether they wish to participate with the study. If at any point during the study participants wish to withdraw consent, they will be able to do this without penalty. Fluency in English and ability to read is a requirement of the study so participants should be able to understand verbal explanations and will have the information sheet thoroughly explained to them if there is any aspect of the material that is unclear.
All members of the research team will have undergone the CBU's standard training in taking consent and deadline with members of the pubic who volunteer for research.

Question 14: Will consent be written?

X Yes

No

The consent forms are attached for adults (**KG_Appendix3.1_Consent_Adult)** and adolescents **KG_Appendix3.2_Consent_Adolescent)**.

Question 15: What will participants be told about the study? Will any information on procedures or the purpose of study be withheld?

PIS forms are tailored for both adults and adolescents, depending on whether they are participating in a behavioural and neuroimaging study:

KG_Appendix2.1_PIS_v2_Behavioural_adults.

KG_Appendix2.1_PIS_v2_Behavioural_adolescents

KG_Appendix2.1_PIS_v2_MRI_adults

KG_Appendix2.1_PIS_v2_MRI_adolescents.

Participants will be told that the study is investigating the behavioural and neural basis for social relationships, social risk and social decision-making. Participants will not be provided with details about every experimental manipulation, especially in cases where social rank of the participant may be manipulated (this may bias their performance in experimental tasks). Participants will be informed that they are welcome to ask questions about the experiment, but full details will only be provided after they have completed all experimental sessions. Full instructions for each task will be provided during each testing session, and participants will be given the opportunity to practice the tasks and to ask questions at any time. Participants will be reminded that they are free to withdraw at any time, without reason. A full debrief about the nature of the experiment will be provided at the task and participants will have the opportunity to ask questions (**KG_Appendix5_Debrief).**

Question 16: Will personally identifiable information be made available beyond the research team?

No. To ensure the confidentiality and anonymity of participants, a participant number will be allocated to each person and data will be recorded in a database according to this number (i.e., not participants' personal information). The analysis between groups will depend on average differences between numerical scores, as will publication of results, thereby protecting the anonymity of participants.

Question 17: What payments, expenses or other benefits and inducements will participants receive?

Participants will be paid £6 per hour (for behavioural testing) and £10 per hour (for fMRI testing), plus contribution to travel expenses (£2.50-£3 rate depending on living proximity from the research unit). This is standard policy at the MRC CBU. If the study is using fMRI, participants will be offered a picture of their brain.

In case of withdrawal, participants will be fully reimbursed for their travel and time.

Question 18: At the end of the study, what will participants be told about the investigation?

All participants will be fully debriefed about the overall aims of the study and how the experimental task has addressed these aims, with particular regard for the explanation of why deception may have been required (**KG_Appendix5_Debrief)**. Any questions surrounding the procedures and experimental setup will be answered. If there is a question that the experimenter could not fully address, the participant can contact the investigator at a later time if any further clarification is needed (contact details of the investigator will be provided).

As we will be screening participants prior to testing and following safety guidelines for fMRI, any harmful side effects are extremely unlikely. However, if distress does occur the experimenter will comfort the participant and (if necessary) will seek assistance of a clinically trained member of staff from the CBU. Participants in our studies may be experiencing varying mood and will be closely observed by the experimenter and any clinical issues will be dealt with immediately.

Question 19: Has the person carrying out the study had previous experience of the procedures? If not, who will supervise that person?

Yes. All researchers involved in this study have considerable experience running behavioural and neuroimaging experiments involving tasks like those proposed here. TD has extensive experience working with individuals with varying levels of low mood and will provide clinical supervision should any issues arise. KG has experience working with individuals of varying low mood and testing adolescents within the MYRIAD study. JS has experience working with individuals of varying low mood imaging experience.

All data collection involving brain imaging methods at the MRC CBU will be supervised by appropriately trained staff (i.e. radiographers for MRI). These staff are appropriately trained and follow standard operating procedures to ensure the safety and comfort of the participants.

Question 20: What arrangements are there for insurance and/or indemnity to meet the potential legal liability for harm to participants arising from the conduct of the study?

Subject to approval by the Insurance Office/Insurer that each individual study is within the scope of the cover provided by the University's insurance policies; indemnity is provided to the University of Cambridge and its employees for legal liability to pay damages for injury caused to volunteers participating in Human Volunteer Studies and/or Clinical Trails under the following insurance policies where applicable.

Question 21: What arrangements are there for data security during and after the study?

All data storage comply with the requirements of the Data Protection Act; information collected will be held according to ethical and legal practice guidelines. Personal identity on these records will be indicated by an ID number rather than any personal details to protect anonymity. Only members of the study team will have access to the data, which will consist of neuroimaging data and behavioural task performance measures. This data will be stored in a locked filing cabinet, and imaging data will be stored in a secure server located at the MRC-CBU. As stated in the consent forms, data will be stored for the MRC-CBU for a maximum of 10 years, in accordance with good research practise.

Fully anonymised data (including de-facing MRIs) may be shared freely with others who request such data, as the MRC-CBU is becoming open to data sharing. These data will be linked anonymised, but the linking will remain held securely by the research team as detailed above.

Signatures of the study team (including date) (Signatures Removed)

Dr. Tim Dalgleish Date: 13/10/2017

Kirsty Griffiths Date: 13/10/2017

Jason Stretton Date: 27/10/2017

Appendix 3.8: Beck Depression Inventory- II (BDI-II: Beck, Steer & Brown, 1996)

BDI-II

Please read each group of statements carefully, then pick out the **one statement** in each group which best describes the way you have been feeling during the **past 2 weeks, including today.** Circle the number beside the statement you have picked. If several statements in the group seem to apply equally well, simply circle the statement which has the largest number. Be sure that you do **not** circle more than one statement for Item 16 (change in sleeping pattern) and Item 18 (change in appetite).

1 Sadness
- **0** I do not feel sad.
- **1** I feel sad much of the time.
- **2** I am sad all the time.
- **3** I am so sad or unhappy that I can't stand it.

2 Pessimism
- **0** I am not discouraged about my future.
- **1** I feel more discouraged about my future than I used to be.
- **2** I do not expect things to work out for me.
- **3** I feel my future is hopeless and will only get worse.

3 Past Failure
- **0** I do not feel like a failure.
- **1** I have failed more than I should have.
- **2** As I look back, I see a lot of failures.
- **3** I feel I am a total failure as a person.

4 Loss of Pleasure
- **0** I get as much pleasure as I ever did from the things I enjoy.
- **1** I don't enjoy things as much as I used to.
- **2** I get very little pleasure from the things I used to enjoy.
- **3** I can't get any pleasure from the things I used to enjoy.

5 Guilty Feelings
- **0** I don't feel particularly guilty.
- **1** I feel guilty over many things I have done or should have done.
- **2** I feel quite guilty most of the time.
- **3** I feel guilty all of the time.

6 Punishment Feelings
- **0** I don't feel I am being punished.
- **1** I feel I may be punished.
- **2** I expect to be punished.
- **3** I feel I am being punished.

7 Self Dislike
- **0** I feel the same about myself as ever.
- **1** I have lost confidence in myself.
- **2** I am disappointed in myself.
- **3** I dislike myself.

8 Self Criticism
- **0** I don't criticize or blame myself more than usual.
- **1** I am more critical of myself than I used to be.
- **2** I criticize myself for all of my faults.
- **3** I blame myself for everything bad that happens.

9 Suicidal Thoughts or Wishes
- **0** I don't have any thoughts of killing myself.
- **1** I have thoughts of killing myself, but I would not carry them out.
- **2** I would like to kill myself.
- **3** I would kill myself if I had the chance.

10 Crying
- **0** I don't cry any more than I used to.
- **1** I cry more than I used to.
- **2** I cry over every little thing.
- **3** I feel like crying but I can't.

11 Agitation
- **0** I am no more restless or wound up than usual.
- **1** I feel more restless or wound up than usual.
- **2** I am so restless or agitated that it's hard to stay still.
- **3** I am so restless or agitated I have to keep moving or doing something.

12 Loss of Interest
- **0** I have not lost interest in other people or activities.
- **1** I am less interested in other people or things than before.
- **2** I have lost most of my interest in other people or things.
- **3** It's hard to get interested in anything.

13 Indecisiveness
- **0** I make decisions about as well as ever.
- **1** I find it more difficult to make decisions than usual.
- **2** I have much greater difficulty in making decisions than I used to.
- **3** I have trouble making any decisions.

14 Worthlessness
- **0** I do not feel I am worthless.
- **1** I don't consider myself as worthwhile or useful as I used to.
- **2** I feel more worthless as compared to other people.

3 I feel utterly worthless.

15 Loss of Energy

0 I have as much energy as ever.
1 I have less energy than I used to have.
2 I don't have enough energy to do very much.
3 I don't have enough energy to do anything.

16 Change in Sleeping Pattern

0 I have not experienced any change in my sleeping pattern.

1a I sleep somewhat more than usual.
1b I sleep somewhat less than usual.

2a I sleep a lot more than usual.
2b I sleep a lot less than usual.

3a I sleep most of the day.
3b I wake up 1-2 hours early and can't get back to sleep.

17 Irritability

0 I am no more irritable than usual.
1 I am more irritable than usual.
2 I am much more irritable than usual.
3 I am irritable all the time.

18 Change in Appetite

0 I have not experienced any change in my appetite.

1a My appetite is somewhat less than usual.
1b My appetite is somewhat greater that usual.

2a My appetite is much less than before.
2b My appetite is much greater than usual.

3a I have no appetite at all.
3b I crave food all the time.

19 Concentration Difficulty

0 I can concentrate as well as ever.
1 I can't concentrate as well as usual.
2 It's hard to keep my mind on anything for very long.
3 I find I can't concentrate on anything.

20 Tiredness or Fatigue

0 I am no more tired or fatigued than usual.
1 I get more tired or fatigued more easily than usual.
2 I am too tired or fatigued to do a lot of things I used to do.
3 I am too tired or fatigued to do most of the things I used to do.

21 Loss of Interest in Sex

0 I have not noticed any recent change in my interest in sex.
1 I am less interested in sex than I used to be.
2 I am much less interested in sex now.
3 I have lost interest in sex completely.

Appendix 3.9: Beck Anxiety Inventory (BAI: Beck, Epstein, Brown & Steer, 1988)

BAI

Below is a list of common symptoms of anxiety. Please carefully read each item in the list. Indicate how much you have been bothered by each symptom during the PAST WEEK, INCLUDING TODAY, by placing an X in the corresponding space in the column next to each symptom.

	NOT AT ALL	**MILDLY** It did not bother me much.	**MODERATELY** It was very unpleasant but I could stand it.	**SEVERELY** I could barely stand it.
1. Numbness or tingling.				
2. Feeling hot.				
3. Wobbliness in legs.				
4. Unable to relax.				
5. Fear of the worst happening.				
6. Dizzy or lightheaded.				
7. Heart pounding or racing.				
8. Unsteady.				
9. Terrified.				
10. Nervous.				
11. Feelings of choking.				
12. Hands trembling.				
13. Shaky.				
14. Fear of losing control.				
15. Difficulty breathing.				
16. Fear of dying.				
17. Scared.				
18. Indigestion or discomfort in abdomen.				

19. Faint.				
20. Face flushed.				
21. Sweating (not due to heat).				

Appendix 3.10: Submissive Behaviour Scale (SBS: Allan, S. & Gilbert, P., 1997)

Participant ID

Date

Below are a series of statements which describe how people act and feel about social situations. Circle the number to the right of the statements which best describes the degree to which a statement is true for you.

Please use the following scale:

	Never	Rarely	Sometimes	Mostly	Always
1. I agree that I am wrong even though I know I'm not	O	O	O	O	O
2. I do things because other people are doing them, rather than because I want to	O	O	O	O	O
3. I would walk out of a shop without questioning, knowing that I had been short changed	O	O	O	O	O
4. I let others criticise me or put me down without defending myself	O	O	O	O	O
5. I do what is expected of me even when I don't want to	O	O	O	O	O
6. If I try to speak and others continue, I shut up	O	O	O	O	O
7. I continue to apologise for minor mistakes	O	O	O	O	O
8. I listen quietly if people in authority say unpleasant things about me	O	O	O	O	O
9. I am not able to tell my friends when I am angry with them	O	O	O	O	O
10. At meetings and gatherings, I let others monopolise the conversation	O	O	O	O	O
11. I don't like people to look straight at me when they are talking	O	O	O	O	O
12. I say 'thank you' enthusiastically and repeatedly when someone does a small favour for me	O	O	O	O	O
13. I avoid direct eye contact	O	O	O	O	O
14. I avoid starting conversations at social gatherings	O	O	O	O	O
15. I blush when people stare at me	O	O	O	O	O
16. I pretend I am ill when declining an invitation	O	O	O	O	O

Total Score 0

Thank you for completing the questionnaire!

SUBMIT

Appendix 3.11: Involuntary Subordination Questionnaire (ISQ: Sturman, E., 2011)

Participant ID

Date

Below are a series of statements that reflect how people may feel about themselves. Please rate the degree to which you agree with each of the statements as they relate to yourself. Please use the following scale:

	Strongly Disagree	Disagree	Neutral - Neither Agree Nor Disagree	Agree	Strongly Agree
1. I feel that I have lost my standing in the world	O	O	O	O	O
2. I feel that I am more confident than other people	O	O	O	O	O
3. I let others criticize me or put me down without defending myself	O	O	O	O	O
4. I feel powerless to change things	O	O	O	O	O
5. I feel completely knocked out of action	O	O	O	O	O
6. I feel that I am more likeable than other people	O	O	O	O	O
7. I do things because other people are doing them rather than because I want to	O	O	O	O	O
8. I feel trapped by my obligations	O	O	O	O	O
9. I feel defeated by life	O	O	O	O	O
10. I feel that I am more desirable than others	O	O	O	O	O
11. At meetings and gatherings I let others monopolize	O	O	O	O	O
12. I can see no way out of my current situation	O	O	O	O	O
13. I feel that life has treated me like a punch-bag	O	O	O	O	O
14. I feel like an outsider in relation to other people	O	O	O	O	O
15. I avoid starting conversations at social gatherings	O	O	O	O	O
16. I want to get away from myself	O	O	O	O	O
17. I feel that I have sunk to the bottom of the ladder	O	O	O	O	O
18. I feel that I am more talented than other people	O	O	O	O	O
19. I am not able to tell my friends when I am angry with them	O	O	O	O	O
20. I feel trapped by other people	O	O	O	O	O
21. I feel that I have lost important battles in life	O	O	O	O	O
22. I feel that I am more competent than other people	O	O	O	O	O
23. If I try to speak and others continue, I shut up	O	O	O	O	O
24. I would like to escape from my thoughts and feelings	O	O	O	O	O
25. I feel that there is no fight left in me	O	O	O	O	O
26. I feel accepted more than other people	O	O	O	O	O
27. I continue to apologize for minor mistakes	O	O	O	O	O
28. I feel trapped inside myself	O	O	O	O	O
29. I feel that my confidence has been knocked out of me	O	O	O	O	O
30. I feel that I am more attractive than others	O	O	O	O	O
31. I listen quietly if people in authority say unpleasant things about me	O	O	O	O	O
32. I would like to get away from who I am and start again	O	O	O	O	O

Total Score 0

Thank you for completing the questionnaire!

SUBMIT

Appendix 3.12: Interpersonal Sensitivity Measure (IPSM: Boyce, P. & Parker, G., 1989)

Participant ID

Date

A number of statements are listed below which relate to how you might feel about yourself and other people. Please indicate by filling in the appropriate circle showing how each one applies to you (whether it is "very like you", "moderately like you", "moderately unlike you" or "very unlike you"). Respond to each statement in terms of how you are GENERALLY and not necessarily just at present. There are no right or wrong answers.

	Very Like Me	Moderately Like Me	Moderately Unlike Me	Very Unlike Me
1. I feel insecure when I say goodbye to people.	O	O	O	O
2. I worry about the effect I have on other people.	O	O	O	O
3. I avoid saying what I think for fear of being rejected.	O	O	O	O
4. I feel uneasy meeting new people.	O	O	O	O
5. If others knew the real me, they would not like me	O	O	O	O
6. I feel secure when I'm in a close relationship.	O	O	O	O
7. I don't get angry with people for fear that I may hurt them.	O	O	O	O
8. After a fight with a friend, I feel uncomfortable until I have made peace.	O	O	O	O
9. I am always aware of how other people feel.	O	O	O	O
10. I worry about being criticized for things I have said or done.	O	O	O	O
11. I always notice if someone doesn't respond to me.	O	O	O	O
12. I worry about losing someone close to me.	O	O	O	O
13. I feel that people generally like me.	O	O	O	O
14. I will do something I don't want to do rather than offend or upset someone.	O	O	O	O
15. I can only believe that something I have done is good when someone tells me it is.	O	O	O	O
16. I will go out of my way to please someone I am close to.	O	O	O	O
17. I feel anxious when I say goodbye to people.	O	O	O	O
18. I feel happy when someone compliments me.	O	O	O	O
19. I fear that my feelings will overwhelm people.	O	O	O	O
20. I can make other people feel happy.	O	O	O	O
21. I find it hard to get angry with people.	O	O	O	O
22. I worry about criticizing other people.	O	O	O	O
23. If someone is critical of something I do, I feel bad.	O	O	O	O
24. If other people knew what I am really like, they would think less of me.	O	O	O	O
25. I always expect criticism.	O	O	O	O
26. I can never be really sure if someone is pleased with me.	O	O	O	O
27. I don't like people to really know me.	O	O	O	O
28. If someone upsets me, I'm not able to put it easily out of my mind.	O	O	O	O
29. I feel others do not understand me	O	O	O	O
30. I worry about what others think of me.	O	O	O	O
31. I don't feel happy unless people I know admire me.	O	O	O	O
32. I am never rude to anyone.	O	O	O	O

Please continue

	Very Like Me	Moderately Like Me	Moderately Unlike Me	Very Unlike Me
33. I worry about hurting the feelings of other people.	○	○	○	○
34. I feel hurt when someone is angry with me.	○	○	○	○
35. My value as a person depends enormously on what others think of me.	○	○	○	○
36. I care about what people feel about me.	○	○	○	○
37. I can usually describe how I feel at the moment in considerable detail.	○	○	○	○
38. I find myself doing things without paying attention.	○	○	○	○
39. I disapprove of myself when I have irrational ideas.	○	○	○	○

Total Score 0

Thank you for completing the questionnaire!

SUBMIT

Appendix 3.13: Striving to Avoid Inferiority Scale (SAIS-I: Gilbert, Broomhead, Irons & McEwan, 2007)

Participant ID

Date

Sometimes people can see life as something of a competition. For example, we often call it the 'Rat Race'. People can vary in how pressured they feel to strive and compete for things that are important to them. Below are a series of statements, which describe how people may think and feel about the need to strive and compete in life. Please circle a number to the right of the statements which best describes the degree to which a statement is true for you.

	Never	Rarely	Sometimes	Mostly	Always
1. To be valued by others I have to strive to succeed	O	O	O	O	O
2. If I make mistakes, I know other people will still like me	O	O	O	O	O
3. Life is a competition	O	O	O	O	O
4. People don't have to succeed to prove themselves to others	O	O	O	O	O
5. People judge you by how well you perform in comparison to others	O	O	O	O	O
6. Win or lose, people accept me anyway	O	O	O	O	O
7. I never feel my place in society is secure but have to strive to prove myself worthy of it	O	O	O	O	O
8. Others will accept me even if I fail	O	O	O	O	O
9. I need to match what other people achieve	O	O	O	O	O
10. People are accepting of me without comparing me to others	O	O	O	O	O
11. If I don't strive to succeed, I'll be left behind everyone else	O	O	O	O	O
12. Whether I succeed or fail, people value me as a person	O	O	O	O	O
13. People compare me to others to see if I match up	O	O	O	O	O
14. I worry about failure because it means you can't keep up and compete with other people in life	O	O	O	O	O
15. I struggle to achieve things so that other people will not look down on me	O	O	O	O	O
16. If I fail at something, I know others will help me try again	O	O	O	O	O
17. Acceptance is something you have to earn and compete with others for	O	O	O	O	O
18. To get on in the world, you have to compete with others	O	O	O	O	O
19. If you don't keep up in looks or achievements others won't bother with you	O	O	O	O	O
20. If I don't strive to achieve I'll be seen as inferior to other people	O	O	O	O	O
21. I don't feel under pressure to prove myself to others	O	O	O	O	O
22. People who can't compete are seen as weak	O	O	O	O	O
23. Even if I do succeed others will not believe it's enough	O	O	O	O	O
24. People accept me whether I'm successful or not	O	O	O	O	O
25. Being competitive gives me a right to life	O	O	O	O	O
26. I don't have to be the best in life to feel wanted	O	O	O	O	O
27. Others have to see me succeed otherwise it's worthless	O	O	O	O	O
28. I don't have to prove myself to feel part of a group	O	O	O	O	O
29. You are loved for what you are, not for what you achieve	O	O	O	O	O
30. You earn respect by out-performing others	O	O	O	O	O
31. Unless you can compete and keep up you get left behind	O	O	O	O	O

Total Score 0

Thank you for completing the questionnaire!

SUBMIT

Participant ID

Date

We are interested in the reasons people feel under pressure to compete. Below are a series of questions which tap this, each beginning with 'If you don't compete with others and succeed.....'. Please circle the number which best describes how much you agree or disagree with each statement.

1. LOSING OUT

If you don't compete with others and succeed...	Don't Agree									Completely Agree
	1	2	3	4	5	6	7	8	9	10
You will not advance in life	O	O	O	O	O	O	O	O	O	O
You will miss out on opportunities	O	O	O	O	O	O	O	O	O	O
You will fall behind others	O	O	O	O	O	O	O	O	O	O

2. OVERLOOKED

If you don't compete with others and succeed...	Don't Agree									Completely Agree
	1	2	3	4	5	6	7	8	9	10
People will overlook you	O	O	O	O	O	O	O	O	O	O
People will not take much interest in you	O	O	O	O	O	O	O	O	O	O
People will pass you over	O	O	O	O	O	O	O	O	O	O

3. ACTIVE REJECTION

If you don't compete with others and succeed...	Don't Agree									Completely Agree
	1	2	3	4	5	6	7	8	9	10
Others will actively reject you	O	O	O	O	O	O	O	O	O	O
Others will push you away	O	O	O	O	O	O	O	O	O	O
Others will be critical and shame you	O	O	O	O	O	O	O	O	O	O
Others will go out of their way to actively exclude you	O	O	O	O	O	O	O	O	O	O

Total Score 0

Thank you for completing the questionnaire!

SUBMIT

Subscales

Loosing Out	0
Overlooked	0
Active Rejection	0

Appendix 3.14: Hewitt-Flett Multidimensional Perfectionism Scale (MPS: Hewitt, P. & Flett, G., 1990)

Listed below are a number of statements concerning personal characteristics and traits. Please read each item and rate from **Strongly Disagree (1)** to **Strongly Agree (7)** by circling your chosen number.

1.	When I am working on something, I cannot relax until it is perfect	1	2	3	4	5	6	7
2.	I am not likely to criticize someone for giving up too easily	1	2	3	4	5	6	7
3.	It is not important that people I am close to are successful	1	2	3	4	5	6	7
4.	I seldom criticize my friends for accepting second best	1	2	3	4	5	6	7
5.	I find it difficult to meet others' expectations of me	1	2	3	4	5	6	7
6.	One of my goals is to be perfect in everything I do	1	2	3	4	5	6	7
7.	Everything that others do must be of top-notch quality	1	2	3	4	5	6	7
8.	I never aim for perfection on my work	1	2	3	4	5	6	7
9.	Those around me readily accept that I can make mistakes too	1	2	3	4	5	6	7
10.	It doesn't matter when someone close to me does not do their absolute best	1	2	3	4	5	6	7
11.	The better I do, the better I am expected to do	1	2	3	4	5	6	7
12.	I seldom feel the need to be perfect	1	2	3	4	5	6	7
13.	Anything that I do that is less than excellent will be seen as poor work by those around me	1	2	3	4	5	6	7
14.	I strive to be as perfect as I can be	1	2	3	4	5	6	7
15.	It is very important that I am perfect in everything I attempt	1	2	3	4	5	6	7
16.	I have high expectations for the people who are important to me	1	2	3	4	5	6	7
17.	I strive to be the best at everything I do	1	2	3	4	5	6	7
18.	The people around me expect me to succeed at everything I do	1	2	3	4	5	6	7
19.	I do not have very high standards for those around me	1	2	3	4	5	6	7
20.	I demand nothing less than perfection of myself	1	2	3	4	5	6	7
21.	Others will like me even if I don't excel at everything	1	2	3	4	5	6	7
22.	I can't be bothered with people who won't strive to better themselves	1	2	3	4	5	6	7
23.	It makes me uneasy to see an error in my work	1	2	3	4	5	6	7
24.	I do not expect a lot from my friends	1	2	3	4	5	6	7
25.	Success means that I must work even harder to please others	1	2	3	4	5	6	7
26.	If I ask someone to do something, I expect it to be done flawlessly	1	2	3	4	5	6	7
27.	I cannot stand to see people close to me make mistakes	1	2	3	4	5	6	7
28.	I am perfectionistic in setting my goals	1	2	3	4	5	6	7
29.	The people who matter to me should never let me down	1	2	3	4	5	6	7
30.	Others think I am okay, even when I do not succeed	1	2	3	4	5	6	7
31.	I feel that people are too demanding of me	1	2	3	4	5	6	7
32.	I must work to my full potential at all times	1	2	3	4	5	6	7

33.	Although they may not say it, other people get very upset with me when I slip up	1	2	3	4	5	6	7
34.	I do not have to be the best at whatever I am doing	1	2	3	4	5	6	7
35.	My family expects me to be perfect	1	2	3	4	5	6	7
36.	I do not have very high goals for myself	1	2	3	4	5	6	7
37.	My parent rarely expected me to excel in all aspects of my life	1	2	3	4	5	6	7
38.	I respect people who are average	1	2	3	4	5	6	7
39.	People expect nothing less than perfection from me	1	2	3	4	5	6	7
40.	I set very high standards for myself	1	2	3	4	5	6	7
41.	People expect more from me than I am capable of giving	1	2	3	4	5	6	7
42.	I must always be successful at school or work	1	2	3	4	5	6	7
43.	It does not matter to me when a close friend does not try their hardest	1	2	3	4	5	6	7
44.	People around me think I am still competent even if I make a mistake	1	2	3	4	5	6	7
45.	I seldom expect others to excel at whatever they do.	1	2	3	4	5	6	7

Thank you for completing this questionnaire

Appendix 4 (Chapter 4)

Appendix 4.1: ROI Analyses of Actual-Ideal Task Factorial ANOVA contrasts

ROI name:	Extra SS:	F statistic:	Uncorrected P:	Corrected P
Main effect of Group				
Precuneus2_-54_40:	0.03:	0.05:	0.822291:	0.999969
dACC2_32_24:	0.58:	1.12:	0.293013:	0.875127
dmPFC4_52_24:	0.43:	0.52:	0.472068:	0.978349
leftAI-28_18_-10:	0.62:	3.04:	0.084891:	0.412733
leftTPJ-48_-56_22:	0.14:	0.58:	0.447937:	0.971690
vmPFC2_48_-18:	0.16:	0.33:	0.566877:	0.993398
Main effect of Discrepancy				
Precuneus2_-54_40:	0.00:	0.00:	0.998461:	1.000000
dACC2_32_24:	0.00:	0.00:	0.960232:	1.000000
dmPFC4_52_24:	0.00:	0.00:	0.970881:	1.000000
leftAI-28_18_-10:	0.01:	0.04:	0.834911:	0.999980
leftTPJ-48_-56_22:	0.00:	0.01:	0.933738:	1.000000
vmPFC2_48_-18:	0.11:	0.22:	0.640890:	0.997855
Interaction: Group x Discrepancy				
Precuneus2_-54_40:	0.01:	0.03:	0.874685:	0.999996
dACC2_32_24:	0.09:	0.18:	0.671268:	0.998738
dmPFC4_52_24:	0.04:	0.05:	0.831076:	0.999977
leftAI-28_18_-10:	0.02:	0.10:	0.750146:	0.999757

leftTPJ-48_-56_22:	0.00:	0.01:	0.915745:	1.000000
vmPFC2_48_-18:	0.01:	0.01:	0.914368:	1.000000

Control Large>Small

Precuneus2_-54_40:	0.03:	0.11:	0.456506:	0.974227
dACC2_32_24:	-0.06:	-0.26:	0.603626:	0.996122
dmPFC4_52_24:	-0.03:	-0.12:	0.549343:	0.991623
leftAI-28_18_-10:	-0.01:	-0.08:	0.530771:	0.989327
leftTPJ-48_-56_22:	0.02:	0.13:	0.447302:	0.971495
vmPFC2_48_-18:	-0.09:	-0.40:	0.656343:	0.998353

MDD Large>Small

Precuneus2_-54_40:	-0.03:	-0.11:	0.545322:	0.991165
dACC2_32_24:	0.07:	0.34:	0.367576:	0.936019
dmPFC4_52_24:	0.05:	0.18:	0.429295:	0.965448
leftAI-28_18_-10:	0.05:	0.38:	0.353586:	0.92704
leftTPJ-48_-56_22:	-0.00:	-0.02:	0.506445:	0.985545
vmPFC2_48_-18:	-0.05:	-0.26:	0.601077:	0.995970

Control Large > MDD Large

Precuneus2_-54_40:	0.06:	0.27:	0.393462:	0.950209
dACC2_32_24:	0.10:	0.45:	0.327967:	0.907882
dmPFC4_52_24:	0.10:	0.36:	0.360060:	0.931319
leftAI-28_18_-10:	0.14:	1.01:	0.158372:	0.644597
leftTPJ-48_-56_22:	0.09:	0.61:	0.270384:	0.849143
vmPFC2_48_-18:	0.07:	0.33:	0.371006:	0.938073

MDD Large > Control Large

Precuneus2_-54_40:	-0.06:	-0.27:	0.606538:	0.996290
dACC2_32_24:	-0.10:	-0.45:	0.672033:	0.998756
dmPFC4_52_24:	-0.10:	-0.36:	0.639940:	0.997821
leftAI-28_18_-10:	-0.14:	-1.01:	0.841628:	0.999984
leftTPJ-48_-56_22:	-0.09:	-0.61:	0.729616:	0.999609
vmPFC2_48_-18:	-0.07:	-0.33:	0.628994:	0.997392

Appendix 5 (Chapter 5)

Appendix 5.1: Demographic Comparison Questionnaire

Comprised of the Narcissistic Personality Inventory (NPI: Raskin, R. & Hall, C., 1981) and Hewitt-Flett Multidimensional Perfectionism Scale (MPS: Hewitt, P. & Flett, G., 1990)

Participant ID_____

The following questionnaires have been designed to assess key aspects of personality.

They have been completed by hundreds of people from all walks of life.

This means we can look at how your results compare to other people of your age group, education level, or to the population as a whole. The results will be presented to you tomorrow.

This inventory consists of a number of pairs of statements with which you may or may not identify.

For example:

A. I like having authority over people

B. I don't mind following orders

Which of these two statements is closer to your own feelings about yourself? If you identify more with "liking to have authority over people" than with "not minding following orders", then you would choose option A. You may identify with both A and B. In this case you should choose the statement which seems closer to yourself. Or, if you do not identify with either statement, select the one which is least objectionable or remote.

In other words, read each pair of statements and then choose the one that is closer to your own feelings. Indicate your answer by writing the letter (A or B) in the space provided to the right of each item. Please do not skip any items.

1. A. I have a natural talent for influencing people.

   B. I am not good at influencing people. 1. _____

2. A. Modesty doesn't become me.

   B. I am essentially a modest person. 2. _____

3. A. I would do almost anything on a dare.

B. I tend to be a fairly cautious person. 3.

_____

4. A. When people compliment me I sometimes get embarrassed.

B. I know that I am good because everybody keeps telling me so. 4.

_____

5. A. The thought of ruling the world frightens the hell out of me.

B. If I ruled the world it would be a better place. 5.

_____

6. A. I can usually talk my way out of anything.

B. I try to accept the consequences of my behavior. 6.

_____

7. A. I prefer to blend in with the crowd.

B. I like to be the center of attention. 7.

_____

8. A. I will be a success.

B. I am not too concerned about success. 8.

_____

9. A. I am no better or worse than most people.

B. I think I am a special person. 9.

_____

10. A. I am not sure if I would make a good leader.

B. I see myself as a good leader. 10.

_____

11. A. I am assertive.

B. I wish I were more assertive. 11.

_____

12. A. I like to have authority over other people.

B. I don't mind following orders. 12.

_____

13. A. I find it easy to manipulate people.

B. I don't like it when I find myself manipulating people. 13.

_____

14. A. I insist upon getting the respect that is due me.

B. I usually get the respect that I deserve. 14.

_____

15. A. I don't particularly like to show off my body.

B. I like to show off my body. 15.

_____

16. A. I can read people like a book.

B. People are sometimes hard to understand. 16.

_____

17. A. If I feel competent I am willing to take responsibility for making decisions.

B. I like to take responsibility for making decisions. 17.

_____

18. A. I just want to be reasonably happy.

B. I want to amount to something in the eyes of the world. 18.

_____

19. A. My body is nothing special.

B. I like to look at my body. 19.

_____

20. A. I try not to be a show off.

B. I will usually show off if I get the chance. 20.

_____

21. A. I always know what I am doing.

B. Sometimes I am not sure of what I am doing. 21.

_____

22. A. I sometimes depend on people to get things done.

B. I rarely depend on anyone else to get things done. 22.

_____

23. A. Sometimes I tell good stories.

B. Everybody likes to hear my stories. 23.

_____

24. A. I expect a great deal from other people.

B. I like to do things for other people. 24.

_____

25. A. I will never be satisfied until I get all that I deserve.

B. I take my satisfactions as they come. 25.

_____

26. A. Compliments embarrass me.

B. I like to be complimented. 26.

_____

27. A. I have a strong will to power.

B. Power for its own sake doesn't interest me. 27.

_____

28. A. I don't care about new fads and fashions.

B. I like to start new fads and fashions. 28.

_____

29. A. I like to look at myself in the mirror.

B. I am not particularly interested in looking at myself in the mirror. 29.

_____

30. A. I really like to be the center of attention.

B. It makes me uncomfortable to be the center of attention. 30.

_____

31. A. I can live my life in any way I want to.

B. People can't always live their lives in terms of what they want. 31.

_____

32. A. Being an authority doesn't mean that much to me.

B. People always seem to recognize my authority. 32.

_____

33. A. I would prefer to be a leader.

B. It makes little difference to me whether I am a leader or not. 33.

_____

34. A. I am going to be a great person.

B. I hope I am going to be successful. 34.

_____

35. A. People sometimes believe what I tell them.

B. I can make anybody believe anything I want them to. 35.

_____

36. A. I am a born leader.

B. Leadership is a quality that takes a long time to develop. 36.

_____

37. A. I wish somebody would someday write my biography.

B. I don't like people to pry into my life for any reason. 37.

_____

38. A. I get upset when people don't notice how I look when I go out in public.

B. I don't mind blending into the crowd when I go out in public. 38.

_____

39. A. I am more capable than other people.

B. There is a lot that I can learn from other people. 39.

_____

40. A. I am much like everybody else.

B. I am an extraordinary person. 40.

_____

Listed below are a number of statements concerning personal characteristics and traits.

Please read each item and rate from **Strongly Disagree (1)** to **Strongly Agree (7)** by circling your chosen number.

46.	When I am working on something, I cannot relax until it is perfect	1	2	3	4	5	6	7
47.	I am not likely to criticize someone for giving up too easily	1	2	3	4	5	6	7
48.	It is not important that people I am close to are successful	1	2	3	4	5	6	7
49.	I seldom criticize my friends for accepting second best	1	2	3	4	5	6	7
50.	I find it difficult to meet others' expectations of me	1	2	3	4	5	6	7
51.	One of my goals is to be perfect in everything I do	1	2	3	4	5	6	7
52.	Everything that others do must be of top-notch quality	1	2	3	4	5	6	7
53.	I never aim for perfection on my work	1	2	3	4	5	6	7
54.	Those around me readily accept that I can make mistakes too	1	2	3	4	5	6	7
55.	It doesn't matter when someone close to me does not do their absolute best	1	2	3	4	5	6	7
56.	The better I do, the better I am expected to do	1	2	3	4	5	6	7
57.	I seldom feel the need to be perfect	1	2	3	4	5	6	7
58.	Anything that I do that is less than excellent will be seen as poor work by those around me	1	2	3	4	5	6	7
59.	I strive to be as perfect as I can be	1	2	3	4	5	6	7
60.	It is very important that I am perfect in everything I attempt	1	2	3	4	5	6	7
61.	I have high expectations for the people who are important to me	1	2	3	4	5	6	7
62.	I strive to be the best at everything I do	1	2	3	4	5	6	7
63.	The people around me expect me to succeed at everything I do	1	2	3	4	5	6	7
64.	I do not have very high standards for those around me	1	2	3	4	5	6	7
65.	I demand nothing less than perfection of myself	1	2	3	4	5	6	7
66.	Others will like me even if I don't excel at everything	1	2	3	4	5	6	7
67.	I can't be bothered with people who won't strive to better themselves	1	2	3	4	5	6	7
68.	It makes me uneasy to see an error in my work	1	2	3	4	5	6	7
69.	I do not expect a lot from my friends	1	2	3	4	5	6	7
70.	Success means that I must work even harder to please others	1	2	3	4	5	6	7
71.	If I ask someone to do something, I expect it to be done flawlessly	1	2	3	4	5	6	7
72.	I cannot stand to see people close to me make mistakes	1	2	3	4	5	6	7
73.	I am perfectionistic in setting my goals	1	2	3	4	5	6	7
74.	The people who matter to me should never let me down	1	2	3	4	5	6	7
75.	Others think I am okay, even when I do not succeed	1	2	3	4	5	6	7
76.	I feel that people are too demanding of me	1	2	3	4	5	6	7
77.	I must work to my full potential at all times	1	2	3	4	5	6	7
78.	Although they may not say it, other people get very upset with me when I slip up	1	2	3	4	5	6	7

79.	I do not have to be the best at whatever I am doing	1	2	3	4	5	6	7
80.	My family expects me to be perfect	1	2	3	4	5	6	7
81.	I do not have very high goals for myself	1	2	3	4	5	6	7
82.	My parent rarely expected me to excel in all aspects of my life	1	2	3	4	5	6	7
83.	I respect people who are average	1	2	3	4	5	6	7
84.	People expect nothing less than perfection from me	1	2	3	4	5	6	7
85.	I set very high standards for myself	1	2	3	4	5	6	7
86.	People expect more from me than I am capable of giving	1	2	3	4	5	6	7
87.	I must always be successful at school or work	1	2	3	4	5	6	7
88.	It does not matter to me when a close friend does not try their hardest	1	2	3	4	5	6	7
89.	People around me think I am still competent even if I make a mistake	1	2	3	4	5	6	7
90.	I seldom expect others to excel at whatever they do.	1	2	3	4	5	6	7

Thank you for taking the time to complete this questionnaire

Appendix 5.2: Self and Others Ratings Sheet

Within-Game Ratings

Participant ID: _____

Below is a list of 20 Adjectives.
To what extent do the following words describe you?

	Not at All				Somewhat				Very Much So	
Kind	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐
Loving	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐
Impressionable	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐
Open-Minded	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐
Bossy	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐
Unstable	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐
Co-operative	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐
Mocking	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐
Embarrasses Others	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐
Protective	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐
A Dictator	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐
Cheerful	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐
Vain	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐
Unpredictable	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐
Conscientious	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐
Unselfish	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐
Hostile	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐
Trustworthy	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐
Friendly	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐
Rude	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐

Below is a list of 10 adjectives. Please rate **your fellow participants**. You might like to think about how they behaved during the game, and your impression of them generally.
To what extent do the following words describe each person?

1. A Dictator

		Not at All				Somewhat				Very Much So
Participant Number	1	☐	☐	☐	☐	☐	☐	☐	☐	☐
	2	☐	☐	☐	☐	☐	☐	☐	☐	☐
	3	☐	☐	☐	☐	☐	☐	☐	☐	☐

4	☐	☐	☐	☐	☐	☐	☐	☐	☐
5	☐	☐	☐	☐	☐	☐	☐	☐	☐

2. Cheerful

		Not at All				Somewhat				Very Much So
Participant Number	1	☐	☐	☐	☐	☐	☐	☐	☐	☐
	2	☐	☐	☐	☐	☐	☐	☐	☐	☐
	3	☐	☐	☐	☐	☐	☐	☐	☐	☐
	4	☐	☐	☐	☐	☐	☐	☐	☐	☐
	5	☐	☐	☐	☐	☐	☐	☐	☐	☐

3. Vain

		Not at All				Somewhat				Very Much So
Participant Number	1	☐	☐	☐	☐	☐	☐	☐	☐	☐
	2	☐	☐	☐	☐	☐	☐	☐	☐	☐
	3	☐	☐	☐	☐	☐	☐	☐	☐	☐
	4	☐	☐	☐	☐	☐	☐	☐	☐	☐
	5	☐	☐	☐	☐	☐	☐	☐	☐	☐

4. Unpredictable

		Not at All				Somewhat				Very Much So
Participant Number	1	☐	☐	☐	☐	☐	☐	☐	☐	☐
	2	☐	☐	☐	☐	☐	☐	☐	☐	☐
	3	☐	☐	☐	☐	☐	☐	☐	☐	☐
	4	☐	☐	☐	☐	☐	☐	☐	☐	☐
	5	☐	☐	☐	☐	☐	☐	☐	☐	☐

5. Conscientious

		Not at All				Somewhat				Very Much So
Participant Number	1	☐	☐	☐	☐	☐	☐	☐	☐	☐
	2	☐	☐	☐	☐	☐	☐	☐	☐	☐
	3	☐	☐	☐	☐	☐	☐	☐	☐	☐
	4	☐	☐	☐	☐	☐	☐	☐	☐	☐
	5	☐	☐	☐	☐	☐	☐	☐	☐	☐

6. Unselfish

	Not at All				Somewhat				Very Much So
1	☐	☐	☐	☐	☐	☐	☐	☐	☐
2	☐	☐	☐	☐	☐	☐	☐	☐	☐
3	☐	☐	☐	☐	☐	☐	☐	☐	☐

Participant Number	4	☐	☐	☐	☐	☐	☐	☐	☐	☐
	5	☐	☐	☐	☐	☐	☐	☐	☐	☐

7. Hostile

		Not at All				Somewhat				Very Much So
Participant Number	1	☐	☐	☐	☐	☐	☐	☐	☐	☐
	2	☐	☐	☐	☐	☐	☐	☐	☐	☐
	3	☐	☐	☐	☐	☐	☐	☐	☐	☐
	4	☐	☐	☐	☐	☐	☐	☐	☐	☐
	5	☐	☐	☐	☐	☐	☐	☐	☐	☐

8. Trustworthy

		Not at All				Somewhat				Very Much So
Participant Number	1	☐	☐	☐	☐	☐	☐	☐	☐	☐
	2	☐	☐	☐	☐	☐	☐	☐	☐	☐
	3	☐	☐	☐	☐	☐	☐	☐	☐	☐
	4	☐	☐	☐	☐	☐	☐	☐	☐	☐
	5	☐	☐	☐	☐	☐	☐	☐	☐	☐

9. Friendly

		Not at All				Somewhat				Very Much So
Participant Number	1	☐	☐	☐	☐	☐	☐	☐	☐	☐
	2	☐	☐	☐	☐	☐	☐	☐	☐	☐
	3	☐	☐	☐	☐	☐	☐	☐	☐	☐
	4	☐	☐	☐	☐	☐	☐	☐	☐	☐
	5	☐	☐	☐	☐	☐	☐	☐	☐	☐

10. Rude

		Not at All				Somewhat				Very Much So
Participant Number	1	☐	☐	☐	☐	☐	☐	☐	☐	☐
	2	☐	☐	☐	☐	☐	☐	☐	☐	☐
	3	☐	☐	☐	☐	☐	☐	☐	☐	☐
	4	☐	☐	☐	☐	☐	☐	☐	☐	☐
	5	☐	☐	☐	☐	☐	☐	☐	☐	☐

Please turn over

Your fellow participants are making the same rating decisions on their own sheets. Where do you think they are ranking you amongst the group for the traits above? Please assign yourself a rank where 1st is the HIGHEST RANKED. *E.g. if you think you will be ranked as the most Cheerful in the group, enter a ranking of '1'.*

1. A dictator
I think I will be ranked _____

2. Cheerful
I think I will be ranked _____

3. Vain
I think I will be ranked _____

4. Unpredictable
I think I will be ranked _____

5. Conscientious
I think I will be ranked _____

6. Unselfish
I think I will be ranked _____

7. Hostile
I think I will be ranked _____

8. Trustworthy
I think I will be ranked _____

9. Friendly
I think I will be ranked _____

10. Rude
I think I will be ranked _____

Thank you for completing the questionnaire

6. Unselfish
I think I will be ranked _____

7. Hostile
I think I will be ranked _____

8. Trustworthy
I think I will be ranked _____

9. Friendly
I think I will be ranked _____

10. Rude
I think I will be ranked _____

Appendix 5.3: Post Scan Believability Questionnaire

Participant ID_____

Thank you for completing the scanning session. We'd like to ask a few questions to get an idea of how you found the tasks.

1. During the scanning session you saw feedback from other participants on aspects of your personality. Did you have any concerns at the time that the feedback you were being shown was not genuine (i.e. actual feedback from other participants)?

I felt satisfied the feedback was genuine □

I felt the feedback was probably fake □

2. During the scanning session you saw how you ranked relative to other members of your demographic group. This was calculated using a range of large data sets and questionnaires. To what extent did you feel this feedback was an objective and accurate measure of your personality?

I felt the method and feedback was probably very accurate □

I felt the method and feedback was probably inaccurate or faked □

3. During the scanning session you completed the Ultimatum game, where you received offers made to you by other participants. Did you have any concerns at the time that these offers were not genuine (i.e. actual offers made by other participants)?

I felt satisfied the offers were genuine □

I felt the offers were probably fake □

Thank you for completing the tasks.

Your experimenter will now provide you with a debriefing sheet and compensate you for your time and any winnings. They will be happy to answer any questions you have about the task.

Appendix 5.4: ROI Analysis of Social Feedback One-Way ANOVA

ROI name: Contrast value: t statistic: Uncorrected P: Corrected P

Pos>Neg

TPJ:	0.03:	0.38:	0.351924:	0.925911
dACC:	0.04:	0.40:	0.346406:	0.922044
dmPFC:	-0.04:	-0.35:	0.635422:	0.997652
precuneus:	-0.03:	-0.32:	0.624884:	0.997214
leftAI:	0.06:	1.13:	0.130531:	0.567959
vmPFC:	0.18:	1.91:	0.029009:	0.161907

Neg > Pos

TPJ:	-0.03:	-0.38:	0.648076:	0.998100
dACC:	-0.04:	-0.40:	0.653594:	0.998272
dmPFC:	0.04:	0.35:	0.364578:	0.934178
precuneus:	0.03:	0.32:	0.375116:	0.940462
leftAI:	-0.06:	-1.13:	0.869469:	0.999995
vmPFC:	-0.18:	-1.91:	0.970991:	1.000000

Pos> None

TPJ:	0.15:	1.57:	0.059165:	0.306444
dACC:	-0.00:	-0.02:	0.508920:	0.985975
dmPFC:	-0.02:	-0.15:	0.561173:	0.992859
precuneus:	0.11:	0.85:	0.199399:	0.736673
leftAI:	0.11:	1.74:	0.042381:	0.228817
vmPFC:	0.23:	1.99:	0.024509:	0.138332

Neg>None

TPJ:	0.12:	1.37:	0.085969:	0.416871
dACC:	-0.04:	-0.36:	0.640989:	0.997859
dmPFC:	0.02:	0.13:	0.448640:	0.971906
precuneus:	0.14:	1.19:	0.118824:	0.531860
leftAI:	0.06:	0.91:	0.181199:	0.698650
vmPFC:	0.06:	0.52:	0.303520:	0.885857

Appendix 5.5: ROI Analysis of Demographic Feedback Depressed Group One-Way ANOVA

ROI name: Contrast value: t statistic: Uncorrected P: Corrected P

Positive>Negative

TPJ:	-0.03:	-0.41:	0.660387:	0.998466
dACC:	-0.01:	-0.06:	0.523861:	0.988348
dmPFC:	-0.02:	-0.15:	0.558014:	0.992545
precuneus:	0.06:	0.70:	0.244051:	0.813381
leftAI:	-0.05:	-0.74:	0.770781:	0.999855
vmPFC:	0.02:	0.17:	0.431477:	0.966233

Negative>Positive

TPJ:	0.03:	0.41:	0.339613:	0.917055
dACC:	0.01:	0.06:	0.476139:	0.979332
dmPFC:	0.02:	0.15:	0.441986:	0.969809
precuneus:	-0.06:	-0.70:	0.755949:	0.999789
leftAI:	0.05:	0.74:	0.229219:	0.790307
vmPFC:	-0.02:	-0.17:	0.568523:	0.993547

Positive>No Discrepancy

TPJ:	0.01:	0.11:	0.457493:	0.974506
dACC:	-0.23:	2.61:	0.008145:	0.030278
dmPFC:	-0.11:	-0.89:	0.811011:	0.999954
precuneus:	0.18:	2.01:	0.023413:	0.132509
leftAI:	-0.08:	-1.32:	0.904790:	0.999999
vmPFC:	0.13:	1.53:	0.063956:	0.327368

Negative>No Discrepancy

TPJ:	0.04:	0.54:	0.295964:	0.878222
dACC:	-0.22:	-2.78:	0.005009:	0.018966
dmPFC:	-0.09:	-0.76:	0.776381:	0.999875
precuneus:	0.12:	1.36:	0.088722:	0.427328
leftAI:	-0.04:	-0.59:	0.722733:	0.999546
vmPFC:	0.12:	1.40:	0.081475:	0.399457

Appendix 6 (Chapter 6)

Appendix 6.1: Participant Information and Response Sheet

Ultimatum Game

Participant ID:_____

The aim of this game is to maximise the number of tokens you have.

You will take the role of either the "Proposer" or the "Responder". The Proposer has a number of tokens and must decide how to split these between themselves and the Responder. The Responder then chooses whether to accept or reject the number of tokens offered. If the offer is accepted, both parties keep the tokens according to the proposed split. However, if the offer is rejected, neither party receives anything, and we move on to the next round.

Your strategy to maximise your tokens is up to you. As Proposer, you could choose to keep most of your tokens and make very low offers, but you take the risk that the offer will be refused. As Responder, you could choose to accept any offer no matter how low, or you could refuse unfairly low offers to deny tokens to the Proposer and thereby encourage higher offers.

Today you will play the role of Proposer. On this questionnaire please write **how many tokens** you would offer fellow participants.

You are playing against participant 1

	Your token offer to participant 1	
	Keeping	Giving
1. You have 10 tokens, each worth 10p		
2. You have 10 tokens, each worth 50p		
3. You have 20 tokens, each worth 10p		
4. You have 10 tokens, each worth 20p		
5. You have 20 tokens, each worth 5p		
6. You have 5 tokens, each worth 10p		

You are now playing against participant 2

	Your token offer to participant 2	
	Keeping	Giving
1. You have 10 tokens, each worth 10p		
2. You have 10 tokens, each worth 50p		
3. You have 20 tokens, each worth 10p		

4. You have 10 tokens, each worth 20p		
5. You have 20 tokens, each worth 5p		
6. You have 5 tokens, each worth 10p		

You are now playing against participant 3

	Your token offer to participant 3	
	Keeping	Giving
1. You have 10 tokens, each worth 10p		
2. You have 10 tokens, each worth 50p		
3. You have 20 tokens, each worth 10p		
4. You have 10 tokens, each worth 20p		
5. You have 20 tokens, each worth 5p		
6. You have 5 tokens, each worth 10p		

You are playing against participant 4

	Your token offer to participant 4	
	Keeping	Giving
1. You have 10 tokens, each worth 10p		
2. You have 10 tokens, each worth 50p		
3. You have 20 tokens, each worth 10p		
4. You have 10 tokens, each worth 20p		
5. You have 20 tokens, each worth 5p		
6. You have 5 tokens, each worth 10p		

You are playing against participant 5

	Your token offer to participant 5	
	Keeping	Giving
1. You have 10 tokens, each worth 10p		
2. You have 10 tokens, each worth 50p		

3. You have 20 tokens, each worth 10p		
4. You have 10 tokens, each worth 20p		
5. You have 20 tokens, each worth 5p		
6. You have 5 tokens, each worth 10p		

Others

We run this task with many groups of people. In the spaces below please indicate offers you would make to individuals in these other groups.

7. You have 10 tokens, each worth 10p	
Token Offer	
Keeping	Giving

8. You have 10 tokens, each worth 50p	
Token Offer	
Keeping	Giving

9. You have 20 tokens, each worth 10p	
Token Offer	
Keeping	Giving

10. You have 10 tokens, each worth 20p	
Token Offer	
Keeping	Giving

11. You have 20 tokens, each worth 5p	
Token Offer	
Keeping	Giving

12. You have 5 tokens, each worth 10p	
Token Offer	
Keeping	Giving

Tomorrow you will all play the role of Responder. You will be shown the offers made to you by your fellow participants and have the opportunity to accept or reject them.

Appendix 6.2. Rejection Rates of Offers by Offer Value

A repeated measures ANOVA was run to investigate whether MDD and Control Groups, as Respondents, differed in the Offers they accepted based on the value of the offer and whether the offer came from an In-Group or Out-Group member. Within-subjects factors were Offer Value (the number of tokens they were offered, 1-10) and Proposer Group (In- Group or Out-Group), the between-subjects factor was Clinical Group with 2 levels (MDD andControls), and the dependent variable was the rejection rate, i.e. what proportion of offers ofthat value were rejected. For rejection rate, Mauchly's Test of Sphericity indicated that the assumption of sphericity had been violated for the interaction between Offer value and Clinical Group ($X^2(44)=172.78$, $p=.000$) therefore a Greenhouse-Geisser correction was used in determining degrees of freedom.

The results indicated that Offer Value had a significant impact on rejection rate, as would be expected ($F(1, 57)=110.898$, $p<.001$, $n_p^2=.638$), in that lower offers were rejected more than higher offers. There was a significant effect of Proposer Group, indicating that rejection rates differed depending on whether the Proposer was a member of the In-Group or the Out-Group ($F(1, 57) = 4.336$, $p=.041$, $n_p^2=.064$) with a higher rejection rate for Out-Group offers (37.8% rejection vs 35.4%) (Figure 1). Contrary to our predictions there was no interaction between Offer Value and Clinical Group ($F(2.174,136.958)=.616$, $p=.555$, $n_p^2=.01$), or Proposer and Clinical Group ($F(1,57)=.434$, $p=.513$, $n_p^2=.007$).

Previous literature has indicated that increased rejection of unfair offers may only be present in samples with moderate and severe depressive symptoms (Robson, 2020). Therefore, the repeated measures ANOVA was rerun including only MDD participants scoring above 18 on

the BDI (bringing the total participants in the MDD group to 22). This analysis found a significant interaction between Offer Value and Clinical Group (F(1, 54) = 2.353, p=.013, n_p^2=.046) indicating that MDD participants with moderate-severe symptoms rejected more unfair offers and less fair offers than Controls (Figure 1).

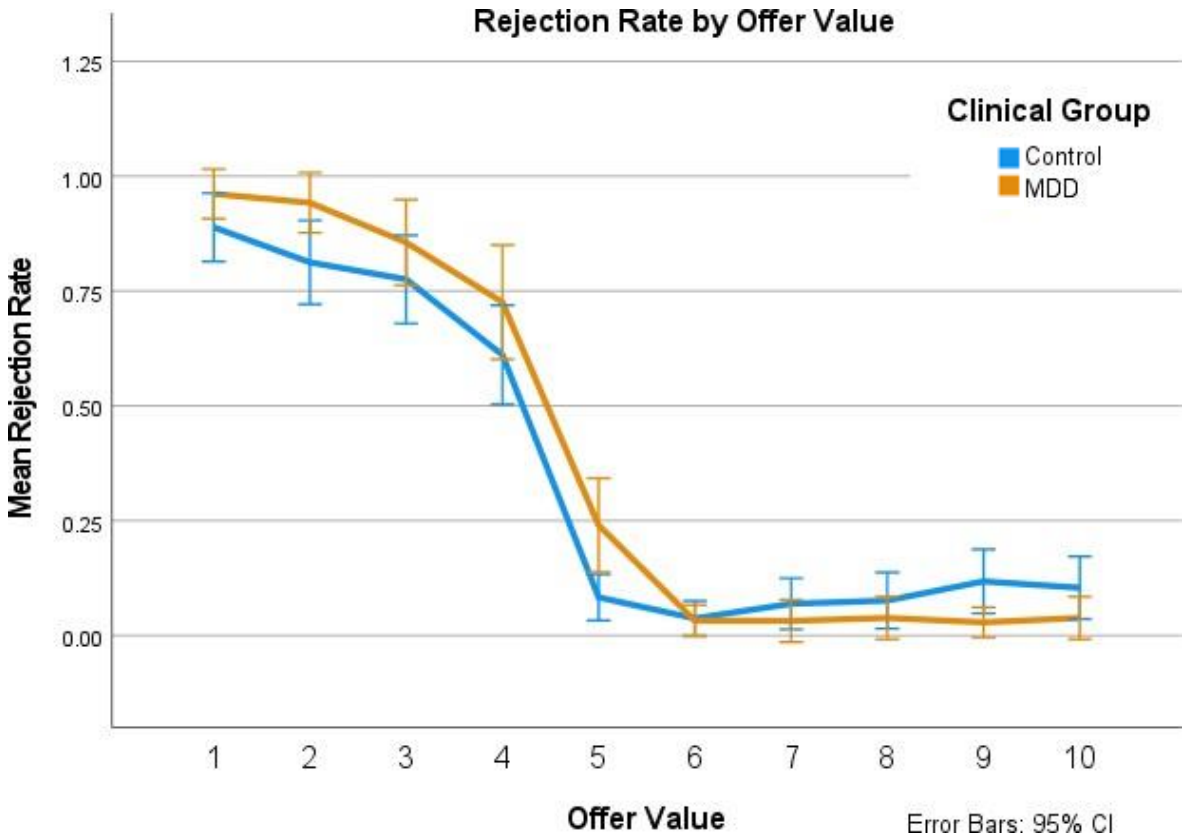


Figure 1. MDD group participants with moderate-severe symptoms rejected unfair offers at a higher rate than Control group participants

Appendix 6.3: ROI data for Fairness ANOVA analysis

ROI name:	Extra SS:	F statistic:	Uncorrected P:	Corrected P
Main effect of ClinGroup				
TPJ:	0.04:	0.10:	0.754381:	0.999780
dACC:	2.77:	6.17:	0.014972:	0.086536
dmPFC:	3.14:	5.65:	0.019625:	0.112120
precuneus:	1.04:	2.07:	0.153508:	0.632095
leftAI:	0.21:	0.86:	0.355168:	0.928108
vmPFC:	0.00:	0.00:	0.982419:	1.000000
Main effect of OfferType				
TPJ:	0.01:	0.03:	0.869673:	0.999995
dACC:	0.30:	0.68:	0.413358:	0.959240
dmPFC:	0.01:	0.01:	0.915586:	1.000000
precuneus:	1.34:	2.67:	0.106091:	0.489778
leftAI:	0.01:	0.03:	0.865758:	0.999994
vmPFC:	0.30:	0.70:	0.405971:	0.956061
Interaction: ClinGroup x OfferType				
TPJ:	0.05:	0.13:	0.719477:	0.999513
dACC:	0.03:	0.07:	0.794254:	0.999924
dmPFC:	0.15:	0.27:	0.604331:	0.996163
precuneus:	0.06:	0.11:	0.738655:	0.999681
leftAI:	0.05:	0.21:	0.648073:	0.998100
vmPFC:	0.02:	0.04:	0.840186:	0.999983

Appendix 6.4: ROI data for Accepted/Rejected ANOVA analysis

ROI name:	Extra SS:	F statistic:	Uncorrected P:	Corrected P
Main effect of Group				
vmPFC:	0.01:	0.03:	0.862242:	0.999993
TPJ:	0.22:	0.68:	0.412484:	0.958874
dACC:	2.44:	5.00:	0.028187:	0.157642
dmPFC:	2.83:	5.91:	0.017375:	0.099825
precuneus:	1.68:	3.25:	0.075278:	0.374732
leftAI:	0.39:	1.81:	0.182028:	0.700476
Main effect of Outcome				
vmPFC:	0.09:	0.19:	0.666315:	0.998620
TPJ:	0.08:	0.26:	0.614374:	0.996711
dACC:	0.41:	0.85:	0.360146:	0.931375
dmPFC:	0.45:	0.93:	0.336581:	0.914743
precuneus:	0.07:	0.14:	0.707553:	0.999374
leftAI:	0.04:	0.18:	0.676545:	0.998855
Interaction: Group x Outcome				
vmPFC:	0.49:	1.04:	0.310805:	0.892835
TPJ:	0.00:	0.01:	0.942565:	1.000000
dACC:	0.14:	0.29:	0.592491:	0.995420
dmPFC:	0.37:	0.76:	0.384550:	0.945655
precuneus:	0.07:	0.14:	0.706449:	0.999360
leftAI:	0.35:	1.63:	0.205327:	0.748157

Appendix 6.5: ROI data for InGroup/OutGroup ANOVA analysis

ROI name:	Extra SS:	F statistic:	Uncorrected P:	Corrected P
Main effect of ClinGroup				
TPJ:	0.31:	0.94:	0.335515:	0.913918
dACC:	2.18:	5.05:	0.027558:	0.154368
dmPFC:	3.50:	7.01:	0.009861:	0.047726
precuneus:	0.85:	1.83:	0.180329:	0.696724
leftAI:	0.34:	1.58:	0.212423:	0.761351
vmPFC:	0.10:	0.25:	0.615350:	0.996761
Main effect of OfferIdentity				
TPJ:	0.49:	1.50:	0.224983:	0.783295
dACC:	0.61:	1.42:	0.237592:	0.803607
dmPFC:	0.86:	1.73:	0.192583:	0.722931
precuneus:	0.44:	0.96:	0.330857:	0.910234
leftAI:	0.12:	0.53:	0.466894:	0.977045
vmPFC:	0.62:	1.64:	0.204830:	0.747210
Interaction: ClinGroup x OfferIdentity				
TPJ:	0.06:	0.17:	0.678176:	0.998889
dACC:	0.17:	0.40:	0.526723:	0.988762
dmPFC:	0.22:	0.44:	0.506985:	0.985640
precuneus:	0.01:	0.03:	0.858786:	0.999992
leftAI:	0.16:	0.76:	0.387240:	0.947065
vmPFC:	0.75:	1.98:	0.163201:	0.656658

MDD > Control

TPJ:	0.25:	0.97:	0.167757:	0.667724
dACC:	0.67:	2.25:	0.013779:	0.079879
dmPFC:	0.84:	2.65:	0.004930:	0.029220
precuneus:	0.42:	1.35:	0.090164:	0.432746
leftAI:	0.26:	1.26:	0.106211:	0.490189
vmPFC:	0.14:	0.50:	0.307675:	0.889882

Appendix 7 (Chapter 7)

Appendix 7.1. Public Goods Game Information Sheet

Instruction Sheet

Please read the instructions below, then press "Finished Reading" on your screen.

You are about to play a game with the 4 other players in the room.

Everyone will start the game with 20 tokens each. There will be many rounds of the game, and at the end we will count up your individual tokens and pay you 5p per token.

How to Play

You decide in each round how many of your tokens to keep for yourself, and how many to put into a group pot along with contributions from the other participants.

Tokens you keep stay in your account.
Tokens put in the Group Pot are all added together, multiplied by 1.5, and then split *equally* amongst the group*, regardless of how much each person contributed.*

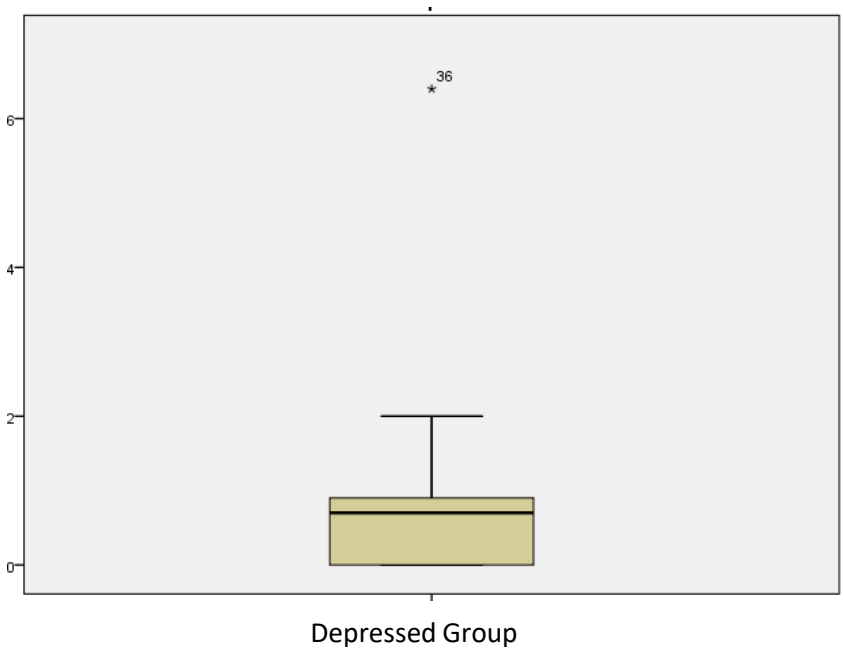
You will then be able to anonymously punish other members of the group, if you wish. This will cost you 1 token, but deduct 2 tokens from them.

These Instructions will be repeated onscreen during the task, and you will have this sheet to refer to.
If you have any questions please ask your experimenter now, then press "Finished Reading".

Appendix 7.2. Boxplots of four excluded datapoints in the PGG Outlier Analysis

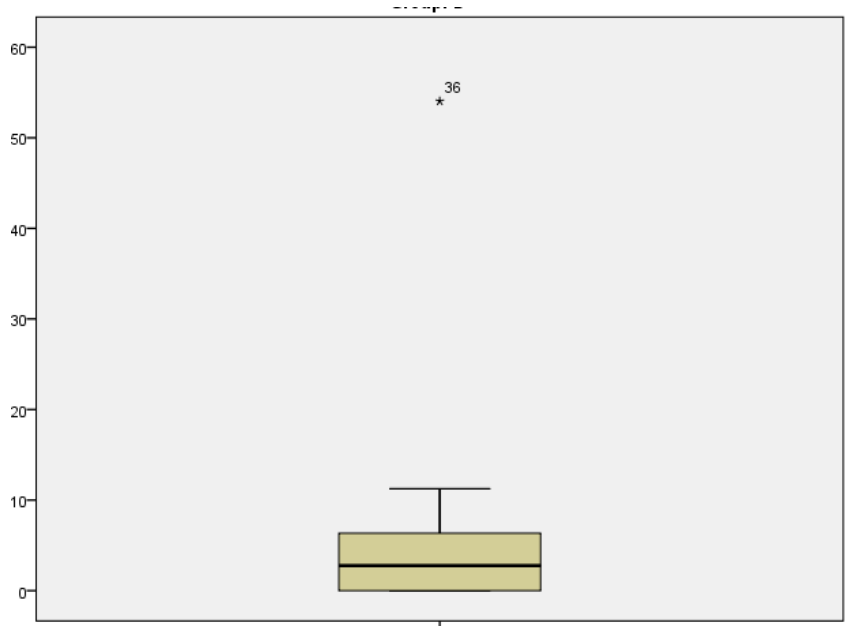
Mean Percentage Contribution Variable

Mean Raw Punishpoints



Mean Percentage Punishpoints

Control Group



Depressed Group

Appendix 7.3. Independent Samples T-tests between genders on PGG Variables

	Male		Female				
Variable	*M*	*SD*	*M*	*SD*	**t**	**df**	**p**
Across Groups							
Final Total	37.52	23.59	43.43	20.33	.977	52	.33
Mean Raw Contribution	9.68	3.55	10.28	4.07	.554	52	.58
Mean Percentage Contribution	40.07	22.18	41.34	18.57	.226	51	.82
Mean Raw Punish points	.80	1.01	.99	.1.27	.553	51	.58
Mean Percentage Punish points	4.86	7.59	4.89	9.74	.010	50	.99
Within Groups							
Controls							
Final Total	38.19	19.49	42.63	16.19	.663	27	.51
Mean Raw Contribution	9.74	3.38	10.53	3.88	.560	27	.58
Mean Percentage Contribution	38.15	22.25	40.62	20.58	.304	27	.76
Mean Raw Punish points	1.07	1.27	.82	.87	-.632	27	.53
Mean Percentage Punish points	6.39	9.88	2.87	3.82	-1.357	26	.18
Depressed							
Final Total	36.80	28.52	44.40	25.01	.704	23	.49
Mean Raw Contribution	9.60	3.91	9.96	4.41	.209	23	.84
Mean Percentage Contribution	42.18	23.10	42.27	16.33	.011	22	.99
Mean Raw Punish points	.51	.53	1.20	1.67	1.255	22	.22
Mean Percentage Punish points	3.32	4.35	7.47	13.93	.905	22	.37

Appendix 7.4. Independent Sample t-tests between groups on Percentage Contribution in Individual Rounds

	Controls		Depressed			
Round	M	SD	M	SD	t	P
1	.47	.23	.56	.33	-1.43	.16
2	.42	.18	.54	.30	-1.71	.09
3	.41	.20	.48	.21	-1.23	.23
4	.42	.21	.45	.23	-.41	.68
5	.34	.21	.45	.25	-1.69	.09
6	.41	.25	.40	.27	.04	.97
7	.41	.25	.35	.22	.81	.42
8	.37	.27	.33	.21	.71	.48
9	.35	.25	.27	.22	1.15	.25
10	.34	.29	.28	.28	.81	.43

Appendix 8 (Chapter 8)

Appendix 8.1: Onscreen Instructions for Participants.

Text reads:
"In this game the goal is to maximise your winnings by collecting tokens, each worth 50p.
You will receive tokens for each balloon you pump up, according to its size. But if you pump it too far it will pop and you'll get nothing for that balloon.
Balloons differ in their maximum size - they can occasionally reach to almost the size of the screen but most will pop well before that.
Press SPACE to pump the balloon, or RETURN to bank the cash for this balloon and move onto the next.

You will play this game twice; once for yourself, and once for your group. When playing for yourself, you keep all tokens and your total is private. When playing for the group, the tokens will be shared equally amongst the group, and your teammates will be informed of how much you won for them, and how often you popped the balloon. Which version you are playing will be clearly indicated on the next screen and throughout the game."