

Understanding Social Behaviour



Macaque behaviour in coordination and cooperation games and the encoding of inequity in striatum

Charlotte Ramona van Coeverden

Newnham College

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Preface

This dissertation was completed within the department of Physiology, Development and Neuroscience under supervision of Professor Wolfram Schultz. Chapters 2, 3 and 4 contain sections of work that were carried out in collaboration with Dr. Raymundo Báez-Mendoza. The extent of this collaboration will also be specified in these chapters

This dissertation is the result of my own work and includes nothing which is the outcome of work done in collaboration except as declared in this preface and specified in the text.

It is not substantially the same as any that I have submitted, or, is being concurrently submitted for a degree or diploma or other qualification at the University of Cambridge or any other University or similar institution except as declared in the Preface and specified in the text. I further state that no substantial part of my dissertation has already been submitted, or, is being concurrently submitted for any such degree, diploma or other qualification at the University of Cambridge or any other University of similar institution except as declared in the Preface and specified in the text. It does not exceed the prescribed word limit for the Biology Degree Committee.

Summary

Social behaviours have been widely studied in behavioural economics and psychology. However, the origins of these behaviours in the brain are poorly understood. In this dissertation I will discuss two main avenues of study which constituted separate projects during my PhD candidacy. The first section contains experiments in which I collaborated with Dr Raymundo Báez-Mendoza on the topic of inequity. The second part includes a study on coordination and cooperation behaviour in macaques.

Inequity is a concept ubiquitous in daily life. It is the difference between one's own reward and that of another. There have been several studies that have suggested inequity affects brain activity. However, few studies have touched upon how this parameter is incorporated in neuronal activity. In the experiments that will be described here, monkeys (*Macaca mulatta*) performed actions to obtain rewards for both themselves and another. The level of inequity in these rewards was manipulated by varying the magnitude of own and other's rewards. We then proceeded to study neuronal activity by means of single neuron recordings in the striatum of two macaques. We found that inequity modulated task related activity in about 32% of recorded striatal neurons. In addition to this study on inequity we also recorded some sessions in which one of the animals made choices with varying rewards for self and other. From these results, I attempted to characterise behaviour with regards to own reward and inequity in choice situations.

Inequity has been considered a contributing factor in explaining cooperation behaviour. Coordination and cooperation are important and frequently observed behaviours. To study coordination and cooperation, I designed an experiment in which the combination of two monkeys' choices determined the rewards for both animals. In this dissertation I attempt to address how the animals perform combined choices (playing together vs. alone) as well as the nature of their behaviour (e.g. pro-social vs. self-interested). The aim of this work was to characterise what type of information the animals use to solve these tasks. This is vital if one is to study these concepts in the brain using macaques as a model. In summary, this work contributes to a better understanding of social behaviour and provides an example of how this social behaviour is computed in the brain.

Chapter 1 – Social behaviour

Social behaviour is a much studied topic in neuroscience as well as in behavioural economics and psychology. However, both how this behaviour stems from neuronal activity and how humans process social information are not very well known. In this dissertation I will discuss two main avenues of study which constituted separate projects during my PhD candidacy. The first section contains experiments in which I collaborated with Dr Raymundo Báez-Mendoza on the topic of how inequity modulates neuronal activity in striatum. The second part includes a study on coordination and cooperation choices in macaques. What binds these two together is that both are concerned with social behaviours. While the experiments designed to study inequity involved one macaque performing actions which resulted in different payoffs for two monkeys, the experiments in which I studied cooperation considered a more complex combination of choices of two animals resulting in outcomes that depended on the other's action. All of this will be explained in later chapters in further detail. Importantly, both studies are inherently social as they involve another conspecific which results in interesting variations in behaviour which are not observed when the conspecific is not present or involved in the task. Before continuing in more detail about the experiments I conducted, it is important to consider the term 'social' in more broad terms and to define more specifically what is meant by this term in this dissertation.

The evolution of social behaviour

There has been much debate about why and how social behaviour exists in animals. An important distinction is that, for a behaviour to be social, it does not need to be selfless. In many cases social behaviours originate from an increase in fitness to the individual rather than the collective. However, to make perfectly clear how we make these distinctions, no discussion of social behaviours would be complete without a discussion of altruism and its limitations.

Altruism or Mutualism

'Pure altruism' is a highly debated and to this day controversial phenomenon. It can be defined as an increase in one animals' utility (or value) as a consequence of a cost to the utility (or value) of another animal (Camerer, 2003). However, an actual act of altruism, or 'self-sacrifice', is not necessary for this to happen, instead it is a mere pleasure in somebody else's fortunate circumstance which may at times lead to altruistic acts. This is also referred to as 'impure altruism'. In impure altruism, acts of altruism may be considered as selfish because the actor experiences an increase in utility because of the act itself (Andreoni, 1990). Even though James Andreoni calls this

‘Impure altruism’, he actually considers this to not be altruistic at all, as it means that the actor is in fact driven by motives other than altruism, namely selfish motives. In conclusion, altruism in its purest form and the motives of animals and humans may be debatable. However, pro-social behaviour is widely observed throughout the animal kingdom. In many cases, it can be explained by long term mutual benefits rather than selfless sacrifice. This is also called ‘mutualism’. Both Altruistic and mutualistic acts are types of social acts, to understand better where these behaviours come from it is important to consider their origins in evolution.

The development of social behaviours under selective pressure

Social behaviour, here defined as behaviour influencing the circumstance of another individual at an initial cost to the performer, was initially unexplained by classical evolutionary theory. Evolution (Darwin, 1859) can be summarised as an iterated two-step process. The first prerequisite is biological variation that comes from variations in DNA and a mixing of DNA to make new combinations. Consequently, a phenotype develops which is a product of interactions that the resulting genes have with the environment. The second step is natural selection. Biological entities that have a higher ‘fitness’ are more likely to reproduce more successfully and, thus, pass their heritable traits on to the next generation. Since Darwin, the assumption that prevails to this day is that the most effective way of improving fitness is to have traits that improve one’s own reproductive success and compete with that of others. This competition was, and is, considered essential to the evolution of traits. The problem with this is that cooperation cannot very easily be explained by individual selection alone.

Thanks to the concept of kin selection we now have a clearer idea of how social behaviours can benefit the fitness of the socially behaving animal (Hamilton, 1964a, 1964b; Mary Jane West, 1975). Kin selection refers to the selection of genetic alleles of an individual’s relatives. The advantage of kin selection, is that it increases the frequency of one’s own gene variants without having to rely on one’s own reproductive success. In simple terms, this means that an agent can affect the reproduction of their own genetic material by means of their own reproductive fitness but also by investing in others that can be assumed to carry some of the same genetic variants. As a result, social behaviours are widely observed throughout the animal kingdom. In humans, we observe many complex, culturally influenced behaviours. Culture fundamentally depends on and is therefore logically tied to social behaviour and cognition. Although an in depth discussion of this is outside the scope of this dissertation, the ubiquity of social behaviour serves to illustrate that people are prone to adaptation to others even when the investment in this behaviour is initially costly. If one wishes

to discuss social behaviour in more depth, it is first important to define a number of terms and concepts associated with social behaviours.

Important concepts of social decision making

Complex social behaviours like cooperation can be broken down into a series of decisions; Stay or move? Save or consume? Share or keep? Behavioural economics is a field of study that is concerned with the factors (e.g. psychological and social) that influence decisions of individuals and or groups. Behavioural economists have developed theoretical frameworks that are widely accepted to explain decisions in humans. The most famous and valuable of these are both the assumption of expected utility maximisation and the clear and concise description of game theory as described by Von Neumann and Morgenstern (Von Neumann & Morgenstern, 1944). Utility theory has yielded many interesting insights into human decision making. However, humans and non-human social animals live in complex social environments. One could argue that human and non-human social agents make most of their decisions under constant social pressure and that it is therefore important to incorporate social variables in the study of decision making (Sanfey, 2007). However, not all social situations are per definition complex. Therefore, it may benefit us to first contemplate the minimal social situation.

The minimal social situation

The word 'social' is used widely and freely, but what does it really mean? In neuro-economics humans and animals have generally been called social if 'social preferences' were evident. Social preferences in turn can be defined as a characteristic of behaviours or motives that indicate an individual preference for others' outcomes. Thus, a 'social preference' means that an individual is 'other regarding' and has a preference with regard to others' rewards (Glimcher, Fehr, Camerer, & Poldrack, 2008). These preferences can be either pro-social, preferring the other to be rewarded, or anti-social, preferring less reward for others. However, in the following paragraph, I will illustrate that social preferences as described in neuro-economics do not necessarily have to play a role in social games.

The 'minimal social situation' was first investigated by Sidowski et al. (Sidowski et al., 1956) and later further characterised in terms of possible social effects on the results (Sidowski, 1957). Sidowski et al. had an approach that was in essence similar to the design of experiments described later in this dissertation. A striking passage was the following: "... no assumption whatever is to be made regarding such concepts as attitude, understanding, awareness etc. If such factors enter the picture

at all, they are to be considered as manifestations of complex habits. Preferably, they will not be encountered at all in the minimal social situation and in any part cannot be part of the definition of social behaviour.”(Sidowski et al., 1956). This constraint on the definition of social behaviour is most striking and seemingly counterintuitive. However, the example of the cross wired train (A.M. Colman, 2013) illustrates the importance of this. Two commuters travel on the same train every day in adjacent compartments. Both compartments have a lever that controls the heating. However, because the wiring in the train is faulty turning the levers controls the heating in the compartment where the other passenger is situated. Turning the lever left heats the compartment and turning it to the right turns the heating down and makes it uncomfortably cold. The first experiments that were done to test whether humans would cooperate under these circumstances (figure 1.1) would, as Colman put it, ‘be hard to get through ethical approval these days’. In this ‘mutual fate control game’, two men would be in different rooms and unaware that their experiment involved another person. The men would then make choices that resulted in positive (monetary) or negative (electrical shocks) outcomes for the other.

Figure 1.1 – Mutual fate control game with binary payoffs

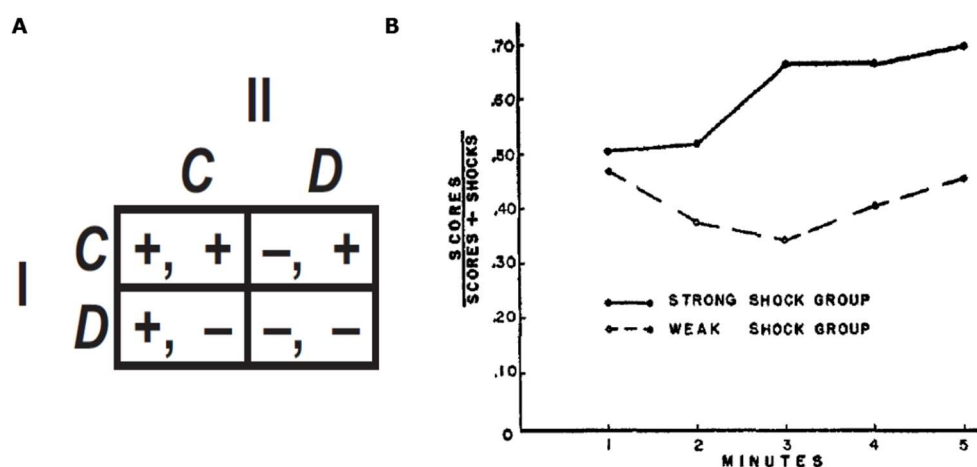


Figure 1.1 Adapted figures from Colman, 2013 (A.M. Colman, 2013) and Sidowski et al. (Sidowski, Wyckoff, & Tabory, 1956) **A** Payoff schematic for a mutual fate game with binary payoffs. Players I and II have choice options C and D. In all cases players control the outcome for the other player but are not aware of this. **B** Sidowski et al. Studied learning in the mutual fate game and found that the strength of the negative outcomes was important for stimulating learning. The important point here is that people can learn to cooperate without knowing they are working together given the right incentives and an equal mutual control of each other’s fates.

Much as in the example of the cross wired train, they only had control over their counterpart’s outcomes but were unaware of this. Each player would have to choose on each trial which button to

press and had the opportunity to learn which button to press over many trials. The researchers observed that a significant amount of cooperation (choosing the positive outcome for the other by both players) was reached within 200 trials for most individuals. This took place even though the subjects' actions had no effect on their own wellbeing whatsoever and the players had no idea that there was another actor involved.

What the minimal social situation teaches us is that there is no need for social awareness or preferences for coordination of choices to occur. When we put this together with the knowledge that we have gathered from other games in which it is apparent that we do have these social preferences the, conclusion is clear. When studying social games it is very important to know how the players play these games. That means that we need to know which parameters enter players' unconscious or conscious perception and to what degree they use these parameters to make choices. We cannot assume that a coordination of choices points to perception of social stimuli or a social preference.

Descriptions of social utility and decision making by economic theory

An approach in behavioural economics has been to study the effect of social context on utility. Utility that incorporates information from others is called social utility. It has been shown that a utility function that incorporates rewards for self and the comparison of this reward to others' rewards (inequity) provides a close fit to behavioural data (Loewenstein, Bazerman, & Thompson, 1989).

Another way to study decisions in social contexts is to use game theory. Von Neumann and Morgenstern can be considered to have formalised game theory in its current form (von Neumann & Morgenstern, 1947). It is important here to distinguish between 'games' and 'game theory'. Games are a collection of strategic scenarios which can be viewed theoretically or tested empirically.

However, game theory is a group of well described mathematical models which try to capture and define various aspects of social decision making. Generally, decisions in games can be very well predicted by the Nash Equilibrium (Dixit & Skeath, 2004). The Nash equilibrium can be described as the joint set of choices in which, given that all other players choices stay the same, the players have no incentive to change their choice strategy (figure 1.2). The practical result of this, is that once the Nash equilibrium strategy is played the player will most likely stay with her current strategy.

Figure 1.2 – The difference between Pareto efficiency and the Nash equilibrium



Figure 1.2 The difference between a pareto-efficient strategy and a Nash equilibrium can be explained by example of a prisoner's dilemma payoff scheme as shown in this diagram. When both players choose 'A' this gives the players the highest outcome without sacrificing the outcome of the other, this is pareto-efficiency (Blue). The rational outcome of the game as predicted by the Nash equilibrium is different (Red). Both players are predicted to choose to maximise their own income by choosing 'B'. In the end if one player chooses 'B' consistently, the other player will only decrease their outcome by choosing 'A'. In other words, there is no reason to choose 'A' unless you are confident that the other player will also choose A. There are also many games in which the pareto-efficient option and the Nash equilibrium overlap.

Another important term in discussing the outcomes of games is pareto-efficiency. A pareto-efficient strategy is played when there is no other option at which a player can become better off without making another player worse off (figure 1.2). The Nash equilibrium can also be applied to strategies. Similar to the 'single choice' definition, a strategy is a Nash equilibrium if each player's strategy is the most optimal response to the other players' strategies. As a result none of the players should have an incentive to deviate from the equilibrium (Camerer, 2003). However, in certain games humans have been known to deviate from the Nash equilibrium. The clearest example of where humans have shown to deviate from the predictions is in the ultimatum game. In the ultimatum game, a 'proposer' has to divide an amount of money between herself and a 'responder'. The responder can then choose whether to accept the amount or reject it. Only if the responder accepts the offer do

both of the players receive the money. If both parties maximise their outcome the proposer should offer the smallest amount possible and the responder should accept any available offer. However, proposers typically offer 40% of their endowment and responders typically reject offers under 20% (Güth, Schmittberger, & Schwarze, 1982). As a result of game theoretical models and the analysis of empirical finding such as these, it was possible to show deviations from classical utility theory in decision making. This proves that humans do not just selfishly maximise their utility but take social factors into account. When removing the 'responder' and just making this participant a passive receiver, the offers of the 'proposer' which is now renamed 'dictator' become markedly less generous, 20%, but significantly higher than the 0% that would be expected if actors are assumed to be utility maximisers. The reduction in the offer means that the 'proposers' were sensitive to the possible rejection of the responder. However, because the 'dictators' when not faced with this threat still give 20% it has been said that this is concrete evidence that humans act altruistically (Camerer, 2003). One could wonder whether the actual amount that people give has any significance. The mean amount that people give in the dictator game is the same amount as the mean minimum amount that responders would accept. It may be that dictators take into account the minimum amount that they would find acceptable when deciding how much of their endowment to offer in the dictator game. As far as I am aware this has not yet been studied. However, studying this kind of motivational framework is complex and beyond the scope of this dissertation.

It is clear that in addition to maximising our personal utility we also incorporate a set of less clearly defined parameters into our decisions that are only evident when the problem is set in a social context involving more than one agent. These other parameters include inequity, fairness and vicarious rewards. By the examination and modelling of these parameters they can be used to expand classical utility theory to explain decisions in a social context.

Economic models that incorporate social variables into conventional utility models

Parameters of social exchange need to be taken into account if we want to describe human decision making in social contexts. This was captured in the social utility functions that were proposed and empirically tested in the late eighties (Loewenstein et al., 1989). Mathew Rabin also proposed a model for social utility, in which fairness and kindness were incorporated to predict the outcomes of economic games (Rabin, 1993). In the conceptual description of this model people are said to reward those who are kind, punish those who are unkind and that these effects are smaller when the material cost of doing so is smaller. Therefore, the model may not be the most parsimonious in

explaining social decisions, as it assumes a knowledge of the others' 'kindness'. Another more influential theoretical framework that takes both self-interest and social variables into account was proposed by Fehr and Schmidt (E. Fehr & Schmidt, 1999). Fehr and Schmidt proposed that preferences are dictated by both one's own payoff but also by aversion to inequity. The inequity of payoffs, as defined by Fehr and Schmidt, are the difference between one's own payoff and a conspecifics payoff (E. Fehr & Schmidt, 1999). The model described by Fehr and Schmidt gives a linear approximation of these utility functions. What the model entails, is illustrated well by examining its mathematical properties.

$$Y = \beta_0 + \beta_1 * W + \beta_2 * \max(Z - W, 0) + \beta_3 * \max(W - Z, 0) + \varepsilon \quad (\text{Equation 1.1})$$

W and Z symbolise own reward and other's reward. The Beta's represent weighting factors which determine the slope of the function. In non-mathematical terms, the beta values determine to which extent own reward, advantageous and disadvantageous inequity are taken into account when determining the utility (Y). If we keep our constant at 0 then we can explain how this model works with an example. For example if a person receives three juice drops but their conspecific receives 5 juice drops the increase in this person's utility is calculated as:

$$Y = \beta_1 * 3 + \beta_2 * \max(5 - 3, 0) + \beta_3 * \max(3 - 5, 0)$$

$$Y = \beta_1 * 3 + \beta_2 * \max(2, 0) + \beta_3 * \max(-2, 0)$$

$$Y = \beta_1 * 3 + \beta_2 * 2 + \beta_3 * 0$$

$$Y = 3\beta_1 + 2\beta_2$$

If we value our own reward at face value and state that $\beta_1=1$, but we devalue this linearly by 20% of every drop the other animal receives more resulting in a $\beta_2=-0.2$. That means that:

$$Y = 3 * 1 + 2 * -0.2 = 3 - 0.4 = 2.6$$

So even though I received 3 juice drops, my increase in utility is only 2.6 because it was devalued by the presence of disadvantageous inequity. This means that negative values of β_2 constitute disadvantageous inequity aversion. However how we respond to advantageous inequity is determined by β_3 . It is the nature of this model to only take into account advantageous 'or' disadvantageous inequity at any given time. In the unique circumstance where the rewards for self and another are equal both inequity terms reduce to zero and only own reward is taken into account.

An alternative theoretical framework was given in the Equity, Reciprocity and Competition (ERC) hypothesis of Bolton and Ockenfels (Bolton & Ockenfels, 2000). The emphasis in the ERC hypothesis

is slightly different because it assumes that people prefer their outcome to be the closest to the mean of all the outcomes rather than minimizing the absolute inequity between individuals.

Whereas in the model of Fehr and Schmidt others' rewards are the driving force for decisions, in the model of Bolton and Ockenfels it only matters how high own rewards lie in this reward distribution.

Why the Fehr and Schmidt model is favourable

The predictive power of these two models was tested with an experiment (Engelmann & Strobel, 2000). This experiment consisted of an allocation of money between two individuals by a person who would receive an intermediate payoff. The choices in this experiment were such that one outcome would maximise the inequity but minimise the subject's difference from the mean payoff and the other option would result in a smaller inequity but a larger deviation from the mean. The ERC hypothesis predicted that subjects would prefer equality of others' payoffs and that the subjects would choose the option with the smallest deviations from the mean. In contrast, the predicted preference by the Fehr and Schmidt model would be to minimise the inequity between payoffs, which is a parameter largely ignored in the ERC hypothesis (Engelmann & Strobel, 2000). Importantly, the model of Fehr and Schmidt was more accurate in predicting the outcome of an experiment which indicated that inequity aversion is an important factor in social decisions.

Combined decisions, social decision making with a twist

In the case of the previously discussed models, social decisions referred to choices between combinations of rewards for self and those for others. However, the experimental data, described in chapters 5 and 6, involve more complex decisions in which the outcomes for each animal is dependent on not only his own but also the other's choice. Here, this type of social decisions are referred to as 'combined decisions'. Combined decision making is a term that arose from studies of the coordination of movement within groups of animals (Conradt & Roper, 2005). However, the definition applies within the types of decisions that will be discussed here. Combined decisions can be defined as "Members of a group (of two or more) choosing individually (but not necessarily independently between actions. They do not aim for consensus but the combined result of their decisions affects the group" (Pyritz, King, Sueur, & Fichtel, 2011). These decisions closely relate to the independent social decisions in the aspect that, in these decisions, the other's outcome depends on a player's choices. The difference is that the animals no longer have full control over the outcomes for both self and other. Two actors are now both responsible for each other's (and their own) outcomes. In summary, combined decisions contain all the elements of other social decisions, but with an added element of the other's choices; they are the basis for coordination and cooperation.

The distinction between Coordination and Cooperation

Coordination and cooperation are similar terms that can both apply across a variety of cases, but there are important distinctions between the two. A similarity is that the objective of the animals is to 'interact', meaning that animal's factor in other social parameters to make choices of the other animal to weigh their own choices. The eventual objective is to maximise the overall outcomes for the animals whether this is an immediate gain or a more delayed steady increase, the actions can only be stable if the result is rewarding. Coordination in particular is important for problems where there are many different options to choose from. It is often more important that all parties settle on any one of these options than it is to choose the one with the best outcome (Camerer, 2003).

Although cooperation is also a form of coordination, it contains an additional level of complexity. Cooperative behaviour involves an initial reduction in payoffs. Even though a choice like this may seem counterintuitive, these choices eventually result in a better payoff over time which will outweigh the initial 'cost' of the behaviour. In addition to this, previous studies have assumed that true cooperative games have a need for communication or collaboration to establish cooperation (Nash, 1953; Noë, 2006). As soon as communication is taken away from a game one could class it as a non-cooperative game (Nash, 1953). To summarise, the clear difference between the two terms is that even though coordination behaviour can be learned by an immediate maximisation of payoffs, cooperation needs other information to overcome the potential initial loss, delay or risk of income. The phenomena of coordination and cooperation have been widely studied with the use of economic coordination and cooperative games. In fact, it was economists that described these problems for the first time and formalised the boundaries of coordination and cooperation by means of economic game theory. In this next section it will become clear that fairly simple economic games can form elegant ways to capture complex social constructs and are therefore a very useful tool when studying both 'single animal' and 'combined' social decision making.

The selection problem of Coordination

Cultural convention contains many examples of coordination in modern society (e.g. writing in a specific direction, driving on one side of the road etc.) An option on which people coordinate their actions is commonly referred to as a focal point of coordination. As described by Camerer, usually it is more important to reach a focal point rather than to converge on an optimal focal point (Camerer, 2003). These types of problems in decision making can be modelled with coordination games. Coordination games are games in which player have to choose corresponding strategies to gain higher payoffs. As described in earlier chapters the outcomes of games can often be predicted by calculating the Nash equilibrium, but in this case the games (per definition) have multiple equilibria (Camerer, 2003). The underlying idea of having to find a solution to this problem can be found in

work as old as over 270 years old by Scottish philosopher and historian, David Hume. In his 'A treatise of human nature' three men have to divide up three different bottles of wine and cannot decide who should take which bottle. Hume simply pointed out that the men should just all have the bottle from their own countries (A. M. Colman, 2003; Hume, Selby-Bigge, & Nidditch, 1978). This problem nicely illustrates the problem of coordination when faced with equally valued options. However it also illustrates the solution, the choosing of a focal point. Focal points in coordination problems are options that are slightly different from the others. A popular hypothesis is that the selection of a focal point is made based on salience (Schelling, 1960). A problem that has been much discussed in economics literature is that whichever way you solve the problem, whether it is salience or some evolved strategy or rule, it does not fit into the mathematical description of rationality. When two options are equal and have equal payoff for both players, there is no way to explain why a player chooses one option over the other on the first trial based on pure game-theoretical rationality (A. M. Colman, 2003). Ultimately, it is difficult to predict which of the equilibria is selected. A possible approach at studying the selection problem is to look at dominating desirable features of options, like for instance payoff-dominance or displays of risk-aversion. Another approach is to look at which option is more desirable from an evolutionary standpoint. A third approach is empirical (Camerer, 2003).

The prisoner's Dilemma – The staple of cooperative scenarios

The prisoner's dilemma is by far the most famous cooperative game. The name of the 'Prisoner's dilemma' comes from an anecdote by A.W. Tucker in 1950 and has been elegantly described in Rapoport's book about conflict resolution (Anatol Rapoport, 1974). Two-prisoner's that are accused of a crime are kept in separate rooms. Each Prisoner gets presented a deal, they can confess and go free if they are the only one to confess. Or if they both confess, they will get a reduced sentence. So whichever option the other chooses, a prisoner is better off confessing. If they do not confess they have a chance of being convicted for the full sentence. If they both do not confess they can only be convicted for minor offenses and will have a shorter sentence. The 'dilemma' is that the outcome if both choose the optimal individual strategy is worse than if both do not choose this strategy. Cooperation in the prisoner's dilemma goes against the expected individual strategy but instead is an act in the interest of the collective. As the prisoner's dilemma is a two-by-two decision making task it is possible to use it to study cooperation in primates. There are other cooperative games, some of these require more than two players (e.g. public goods games) but those are beyond the scope of the work in this thesis. In summary of the last few paragraphs, coordination and cooperation games each have their own unique points of interest. A prisoner's dilemma could be described as a coordination game with two unequal equilibria. However what makes one of these

equilibria unstable is a temptation to choose the suboptimal coordination option. In chapters 5 and 6 experimental data will be shown which demonstrates the difference between coordination and cooperation by contrasting these games.

So far this dissertation has covered the concepts that are necessary to understand experiments that are concerned with social behaviour. Next, it is important to consider what is already known in this field and what types of behaviour can be observed in human and non-human primates.

Social behaviour in Human and Non-human Primates

Humans display a large range of social behaviours. Society depends on a widespread consensus on how to treat each other and is sustained by a willingness to submit others to costly punishment when they do not follow the social norm. Some examples are our juridical and tax systems. With so many levels of cultural influence and upbringing it can be hard to distinguish what the root of our social preferences is. A way to study social behaviour is to look at our closest ancestors in the animal kingdom, primates. By studying primates we can apply more invasive measures, allowing us to study neuronal activity while the animals perform behaviours analogous to those seen in humans. Other advantages of using primates as a model rather than humans is that they can perform more complex behaviours than for instance rodents, another much used model. Other relevant factors are that they are social animals and that they can be trained to perform high amounts of trials incurring a high level of statistical power to show small changes in behaviour. It is for these reasons that primates make an excellent model to study social decision making and the encoding of social preferences in the brain.

The term social preferences has been used to discuss preferences of groups or societies (Glimcher et al., 2008). Here I use this term to indicate individual preferences that concern the rewards of collective own and other's rewards and therefore contribute to the preferences of the group or pair. In a similar fashion, the term 'social behaviour' relates to behaviours which influence the circumstance of one or more conspecifics (for better or worse), sometimes at a cost to the performer. It is logically unlikely that complex social behaviours have evolved *de novo* in humans. In support of this idea, non-human primates like macaques pay joint attention to social stimuli (Emery, Lorincz, Perrett, Oram, & Baker, 1997) and show a reflexive behaviour of looking in the same direction as others (Deaner & Platt, 2003). They are also capable of social learning and coordination (S. F. Brosnan, Wilson, & Beran, 2012; Subiaul, Cantlon, Holloway, & Terrace, 2004). Primates have elaborate social structures with clear rules and social dominance hierarchies. Any animal that does

not comply with the social norm is quickly and harshly punished; even relatives of the principal protagonist can be involved in this process (Clutton-Brock & Parker, 1995). Social behaviour, for instance cooperation, can also lead to larger rewards and higher chances of survival. Brown Capuchins for instance are known to share rewards more readily if they were obtained by a shared effort (de Waal & Berger, 2000). Marmosets have even been known to spontaneously provide food for others (Burkart, Fehr, Efferson, & van Schaik, 2007). As primates are our closest ancestors in the animal kingdom, the study of primate behaviours provides us with insight into how these behaviours may have evolved. In addition to this, primates are also used as models to study neuronal activity related to these behaviours. This reinforces the necessity for understanding these behaviours in primates even further. Much research has been concerned with social cognition in primates (Tomasello & Call, 1994). In this dissertation the focus lies on behaviours that rely on these cognitive abilities.

Examples of primates' social capabilities come from research on gaze perception. For instance, the perception of others' vision as a measure of 'Theory of Mind' provides an interesting conceptual framework. Some studies have pointed out that primates have an awareness of what others see and make choices accordingly (Flombaum & Santos, 2005). It is also apparent that primates are not only aware of the other's gaze but can also integrate this with information about identity, social status and the other's emotional state. On a more sophisticated behavioural level, monkeys can work together as a result of their social cognitive capabilities. For this to happen, the animals use their social cognitive capabilities to gather information about conspecifics but they also need to factor in information about reward and punishment to decide how to act. In this dissertation, I will focus in particular on inequity and how information about this important parameter is taken into account. It is therefore of importance to also take a special interest in attitudes towards inequity.

Inequity related behaviour in humans

Human children as young as three years old dislike disadvantageous inequity (LoBue, Nishida, Chiong, DeLoache, & Haidt, 2011). This was also confirmed later in a study, which showed that children from four to seven years old rejected disadvantageous inequity but accepted advantageous inequity (Blake & McAuliffe, 2011). However this same work showed that children as young as eight years old also start to show aversion to advantageous inequity. In adult humans, inequity aversion has been described in much detail. In psychology research it has also been proposed that inequity prompts responses of reciprocity in humans that restores equity in pairs (Leventhal, Weiss, & Long, 1969). One of the most elegant descriptions of inequity preferences showed that a function containing own reward and separate terms for advantageous and disadvantageous inequity fitted

the data in social decision making closely (Loewenstein et al., 1989). In this same paper, it was also clear that even though disadvantageous inequity stayed relatively constant, advantageous inequity behaviour was dependent on the relationship between the individuals and the type of dispute that they were deliberating. Most of the subjects in these studies exhibited an aversion to advantageous inequity or at worst only a weak preference. The importance of social exchange in behaviour related to inequity is strengthened by the finding that people have egocentric ideas of fairness before going into a negotiation which is then mitigated after bargaining (Thompson & Loewenstein, 1992). Summarising, humans generally respond negatively to both advantageous and disadvantageous inequity. However, responses to advantageous inequity arise at a different age and differ from those to disadvantageous inequity.

Single option or choice context affects the relative weights of social utility

It is important to note here that there can be a discrepancy in behaviour towards inequity based on the informational context in which the options are presented. When viewing options with rewards for self and others independent of each other a lot of weight is placed upon the discrepancy between the two options. This is different when a choice is presented with two combinations of rewards for self and other. In choice behaviour more weight is placed on the difference in the amount for the actor (Bazerman, White, & Loewenstein, 1995). This means that choices in social rewards can't always be predicted by the subjective rating of choice options separately and changes in utility as a result of reward inequity can be overshadowed by the utility for personal reward only when decisions need to be made between choice options.

Inequity attitude in non-human primates

Non-human primates have also shown many signs of reacting negatively to inequity. In particular disadvantageous inequity has been shown to evoke reactions of rejecting offers at their own expense. For example chimpanzees, rhesus monkeys and capuchin monkeys have been seen to react negatively or even reject unequal pay (S. Brosnan, 2006; Sarah F. Brosnan & de Waal, 2003). Interestingly this social comparison has been studied in a longitudinal study in rhesus macaques which showed that much like in humans older monkeys show rejections of disadvantageous inequity but the same monkeys when they were younger monkeys did not (S. F. Brosnan, Hopper, Lambeth, Schapiro, & Bernacky, 2012). This confirms that just like in humans inequity attitude develops over time in primates.

Figure 1.3 – Previous data displayed difference in reaction time for other’s reward

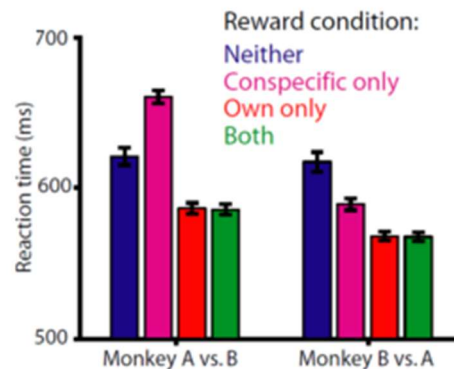


Figure 1.3 Figure in Báez-Mendoza et al. (2013) (Báez-Mendoza, Harris, & Schultz, 2013) Data from a previous experiment already showed that monkeys had a different response when acting to gain reward for another monkey as compared to acting to gain no rewards. One could say there is an effect of other’s reward but only when there is no reward for the actor.

Attitude to inequity and cooperation

Inequity is an important parameter in our environment that we generally find aversive. It is mostly negative inequity that is easily understood and widely experienced by most people. What is more difficult to understand, is that positive inequity is also aversive (Loewenstein et al., 1989). A possible explanation is that positive inequity aversion helps us cooperate which in turn facilitates gaining larger rewards over time. A comprehensive analysis of how caring about equity can resolve how people behave in competitive bargaining situations was done by Fehr and Schmidt in 1999 (E. Fehr & Schmidt, 1999). One of their main findings was that, whether people would be more prone to act selfishly or fair in markets, depended on the economic climate, the rules of punishment and the distribution of social preferences. Another analysis by Fehr and Fischbacher also pointed out that social preferences are important to understand cooperation and collective action (also called coordination here) (E. Fehr & Fischbacher, 2002). The same authors also pointed out that reciprocity and fairness are important. If treated fairly people would cooperate voluntarily (E. Fehr, Fischbacher, & Gächter, 2002). This is in accordance with another study in which it seems that half of the subjects could be classed as ‘conditional cooperators’, people who contribute according to what others contribute in a public goods game (Fischbacher, Gächter, & Fehr, 2001). In addition to these clues from behavioural economics and mathematical modelling about inequity and cooperation, there are also biological and evolutionary arguments for believing the two are intricately connected.

Sarah Brosnan hypothesised that inequity aversion coding in the brain evolved together with cooperation in social species (S. Brosnan, 2006). She has added to this theory, writing that inequity aversion could have created a selective pressure for cooperative individuals because it increases payoffs in cooperative exchanges (S. F. Brosnan, 2011). An increase in cooperative exchanges could be linked to an increase in reproductive success; this is especially the case in cooperatively breeding species like humans. In conclusion, inequity aversion is an important factor in social exchange and cooperation. This suggests that the neuronal processing of inequity is a prerequisite for social exchange. Based on the behavioural data discussed in the previous paragraph, this seems to be the case.

Coordination and Cooperation behaviour in primates

Coordination in humans is influenced by factors within individuals. Important parameters that distinguish one player from another can be: communication, player sequence, advantages in pay-out or risks, cues to bargaining power (e.g. reputations) (Camerer, 2003). An interesting point in the evidence surrounding how humans behave in coordination games is that the combination of dilemmas presented in a problem can influence the outcome in coordination. In these cases pareto-dominance is not always the best predictor for which coordination solution will arise (Cooper, Dejong, Forsythe, & Ross, 1990). Another very important result is that not only the game itself but previous games that are played can set an important precedent, influencing current games. If players have played a weak-link game efficiently (obtaining the largest 'collective' reward) this precedent can improve cooperativeness in a subsequent prisoner's dilemma (Knez & Camerer, 2000). When played iteratively, reciprocity and punishment can influence the amount of cooperation, as described in earlier work by Trivers (Trivers, 1971).

Cooperative and coordination behaviours are not unique to humans and have been studied in other animals (Stephens, McLinn, & Stevens, 2002; Viana, 2010). However, none of these studies of cooperation are as relevant to the understanding our own origins of cooperation as those of our closest relatives, primates. It has been shown without a doubt that many types of primates can coordinate their actions to receive higher rewards. Brosnan et al. did a very interesting comparative study of coordination between Capuchins, macaques and humans (S. F. Brosnan, Wilson, et al., 2012). In this study the coordination game is played in a synchronous and asynchronous version. The synchronous version is more difficult because the players do not have information about what their conspecific is choosing. Most macaque dyads managed to play the game in the synchronous version as well as the asynchronous which was more similar to the performance of humans, whereas Capuchins, which are less closely related to us, did not manage to perform this task and relied much

more on seeing the actions of their conspecific. A similar approach with our closest relative, the Chimpanzee, showed a similar result. Chimpanzees could coordinate for larger rewards with or without seeing each other (Bullinger, Wyman, Melis, & Tomasello, 2011). Importantly, the chimpanzees adopted a strategy in which one monkey would go first and then would only communicate if the second was slow to follow. This shows that coordination does not necessarily require communication.

Another typical task that has been done with many primates is a task in which two animals have to pull two handles at the same time to gain rewards. In one study, Capuchin monkeys were shown to pull the handles together. However, they also pulled the handles when they were alone and did not register when the other was at the other side of the apparatus. The monkeys were therefore concluded to be able to perform the task but only as monkeys that were acting 'by themselves' and just happened to sometimes be successful at pulling at the same time as others (Chalmeau, Visalberghi, & Gallo, 1997). In a later evaluation of this same task capuchins were found to glance at their partners significantly more and to pull at higher rates when their partner was present rather than absent (Mendres & de Waal, 2000). Whether there was an inherent difference between these two sets of animals or whether the task design was responsible for the differences of outcomes is unclear. A similar task, when done with marmosets yielded more interesting results as asymmetrical food delivery made it necessary for the animals who received the food to share this food (Werdenich & Huber, 2002). Food sharing in marmosets is common (Burkart et al., 2007) but it is possibly less likely that this paradigm would work with macaques for whom food sharing is less common. In a recent neurophysiological study the interaction between macaques has been studied in a prisoner's dilemma (Haroush & Williams, 2015). In this task macaques cannot see each other's choices. So any communication or use of social information is excluded from having an effect. As a result animals defect on the majority of trials and mutually cooperate on less than 25% of trials. So far, there have been no studies published that show whether macaques can cooperate more than chance level when being allowed to use information from seeing the other animal's choices. The importance of these studies is to illuminate the boundaries of what we can study in primates. However when we want to bridge the gap to how their and our brains perform these functions we need to pick apart the exact nature of these behaviours. It is absolutely crucial that we know which information is actually used to solve these tasks by primates to better inform correlates seen between neuronal activity and cooperative behaviour. We currently do not know what information primates use to perform these tasks or whether macaques can even significantly cooperate in a prisoner's dilemma.

Use of strategy in cooperative games

In the studies of cooperation there are a couple of strategies that have been hypothesized to increase cooperation. It seems that a lot of the reasoning behind strategies stems from games which are simulated as blinded games in which players are not assumed to have full access to the other's choices but instead use information from previously played rounds in repeated games. It follows that strategies are therefore a phenomenon of the individual rather than the collective. Strategies can therefore logically also apply in non-social situations and do not necessarily depend on the presence of another agent. Modelling of strategies can tell us which strategy would perform best in theory. A section of Axelrod's book on the evolution of cooperation (Axelrod, 1984) deals with this. Axelrod described how he initiated a computer tournament for which he invited professional game theorists to design a strategy that they thought would perform best in the prisoner's dilemma. The winner from this tournament was the tit for tat strategy which was submitted by Rapoport. Tit for tat is a simple strategy based on a delayed mimicking of the other's choices. It starts with cooperation and then continues by choosing whichever choice the other chose on the previous round.

The tit for tat strategy has also been known to increase cooperation in humans (Oskamp, 1971; Wilson, 1971). Although there are reasons to assume tit for tat as a strong candidate to improve cooperation it also has its critics. The tournament was actually called into question as a good method to test the effectiveness of strategies (Amnon Rapoport, Seale, & Colman, 2015) and other methods that allowed for more noise in the simulation showed that a win-stay lose shift strategy can actually perform better than a tit for tat strategy (Nowak & Sigmund, 1993). Win-stay lose-shift responds to the outcome of own choices rather than mimicking the other's choices. The rule in this strategy is also relatively simple, if a player receives more or the same reward on a trial the player stays with the choice that was made, if there is a loss of income then a switch takes place to the other choice option. The strength of this model is that one defection between two tit for tat players would result in a long period of unilateral defection switching between players, whereas in win-stay lose-shift players one defection will instead just lead to one trial unilateral defection after which both animals could return back to stable cooperation.

Another way to establish cooperation that is more stable than standard TFT is to make the strategy more forgiving to mistakes these more lenient strategies have been called 'generous tit for tat', 'lenient tit for tat' or 'tit for two tats' but they all have the same goal which is to keep cooperating once mutual cooperation has been established. I would argue that this forgiving behaviour can also be extended to win-stay lose-shift strategies and can be generalised as behavioural 'perseverance'.

Perseverance can be described as a continued repeating of choices independent of the (immediate) outcome. As a strategy that is played all the time this would of course not be favourable as a permanent strategy as it would make the player severely vulnerable to exploitation. However, as a strategy that is applied under certain circumstances it can also improve the reputation of the player or allow for mistakes by the other player with minimal losses during relatively stable cooperation. In coordination perseverance on one option can make it easier for the other to predict which outcome to choose which could potentially facilitate both coordination and cooperation.

In summary so far, I have discussed concepts of importance to understanding social behaviour. We have also considered social behaviours in both human and non-human primates. Following from this, the next section of the introduction will contain what we know so far of how the brain is involved in processing of social information and social behaviours.

The social brain

The current empirical evidence on the neuronal and neural processing of social behaviour is limited but some work has been done to advance this field of study. It is important to consider this work and let it serve as a framework in which to consider the experiments conducted for this dissertation. It has been suggested that the size of our brains correlates with the ability to interact socially and results in larger group sizes in animals with larger brains (Dunbar, 1992; Reader & Laland, 2002). Alternatively, changes in social context have been shown to correlate with an increase in grey matter in mid-superior temporal sulcus and rostral prefrontal cortex in primates, possibly showing that changes in social environment impact brain structure and function (Sallet et al., 2011). Thus, it is important to keep in mind that, even though we are interested in how our brains perceive and shape our social environment, there may also be an effect in the opposite direction where our social environment has an impact on our brain's structure and function. In this next section we will consider which areas in the brain are involved in social processes and what we know about how the brain regulates social behaviour.

Cortex

Ventromedial prefrontal cortex (vmPFC) has long been regarded instrumental to decision making in both social and non-social decisions. Patients with bilateral vmPFC lesions have severe impairments in decision making without losing their general intellectual problem solving skills (Bechara, Tranel, & Damasio, 2000). In gambling tasks, these patients choose options with larger immediate payoffs even when faced with future losses. These patients have been shown to do this because they are insensitive to future consequences, irrespective of their positive or negative nature (Bechara et al.,

2000). More remarkably, this is not because of a lack of knowledge or understanding. Patients with lesions to ventromedial regions have been known to display sociopathy even though all of their learned knowledge of possible response options and their consequences are intact (Saver & Damasio, 1991). Dorsomedial prefrontal cortex has been implicated in social behaviours as it has been shown to process the discrepancy of own preferences those of others. Activity in this area was correlated with a subsequent change in preferences due to social manipulation (Keise Izuma & Adolphs, 2013).

In addition to processing subjective value (Kringelbach, O'Doherty, Rolls, & Andrews, 2003; Padoa-Schioppa & Assad, 2006) and risk (O'Neill & Schultz, 2010), the orbitofrontal cortex has also been suggested to have an important role in decision making. Patients with lesions to the orbitofrontal cortex have been reported to be unable to shift their behaviour and adapt their strategy even though they can report shifts in contingencies (Edmund T. Rolls, 2000). It has been hypothesised that the OFC's role is the computation of value signals for choice options that can then be compared and used to make decisions (Wallis, 2007). While the OFC is likely to have a role in social decision making, this role does not seem to be different than the encoding of value it does for other value based decisions. This follows from a study in which neurons in the OFC and Anterior cingulate gyrus (ACCg) and sulcus (ACCs) were recorded in a task in which monkeys had to allocate rewards to self and another (S. W. C. Chang, Garipey, & Platt, 2013). OFC neurons were observed to predominantly encode rewards delivered to the monkey himself, while ACCg neurons encoded rewards to both other and self. The ACCs neurons signalled rewards to the other or when neither received a reward.

Amygdala

The amygdala has also been implicated as being of importance in social behaviour. A study in which bilateral amygdalectomies changed social behaviour suggested that animals were more aggressive and lost their dominance after the surgeries. (Rosvold, Mirsky, & Pribram, 1954) In another study, neuronal activity was recorded in amygdala with radio telemetry during social interactions between primates. Neuronal activity varied with the social interaction that the monkey was involved in. The amygdala neurons were more active during activities with sexual and aggressive behaviours and less during grooming (Kling, Steklis, & Deutsch, 1979). Interestingly, in yet another study, three patients with complete bilateral amygdala damage judged faces of unfamiliar people as more approachable and trustworthy than controls. The same deficiency did not seem to be the case for written descriptions of the same people (Adolphs, Tranel, & Damasio, 1998). This also confirms a body of evidence from neuroimaging that shows that amygdala is involved in recognising emotion in facial expressions (Morris, deBonis, & Dolan, 2002; Morris et al., 1998; Morris et al., 1996) and social gaze

(Hoffman, Gothard, Schmid, & Logothetis, 2007) even when the actual conscious perception of seeing the face is suppressed by binocular rivalry (Williams, Morris, McGlone, Abbott, & Mattingley, 2004). Thus, the amygdala seems to play a role in recognition of facial expressions, yet it had not been clearly implicated in social decision making until more recently. In 2005 a study by Chang and Platt basolateral amygdala neurons were found to encode values of rewards of own and other's rewards and social preference (Steve W. C. Chang et al., 2015). This very interesting finding was not known when we designed our study that was designed to study striatal neurons. What makes the study by Chang et al. even more interesting is that the neurons that encoded values of rewards only did so in free choice trials which makes a stronger case for the recruitment of amygdala in social decision making.

Mirror Neurons

An important class of neurons that is important to social cognition and should be mentioned here, are mirror neurons that encode visual feedback of goal achievement and view based action encoding (Rizzolatti & Craighero, 2004). These neurons can be found in area F5 of primate premotor cortex in macaques (Caggiano, Giese, Thier, & Casile, 2015). Interestingly the neuronal encoding of a viewed action is modulated by the value of the object that the other is grasping (Caggiano et al., 2012). In humans, fMRI research has confirmed that anterior intraparietal sulcus was suppressed by goal directed activity independent of the trajectory that was taken. Even though mirror neurons are important for awareness of other's intentions and goals it is not clear how they would be affected in social decision making.

Striatum

Another important structure that is clearly involved in processing of social information, is the caudate nucleus of the striatum. The striatum is known for reward and action processing (Apicella, Scarnati, Ljungberg, & Schultz, 1992; X. Y. Cai, S. Kim, & D. Lee, 2011; Cromwell, Hassani, & Schultz, 2005; Cromwell & Schultz, 2003; Hikosaka, Sakamoto, & Usui, 1989b; Hollerman, Tremblay, & Schultz, 1998; Lau & Glimcher, 2007, 2008; Kazuyuki Samejima, Yasumasa Ueda, Kenji Doya, & Minoru Kimura, 2005; K. Samejima, Y. Ueda, K. Doya, & M. Kimura, 2005; Schultz, Apicella, Scarnati, & Ljungberg, 1992) and has also been implicated in neural encoding of social parameters like inequity and social rewards (Fliessbach et al., 2012; Fliessbach et al., 2007; K. Izuma, Saito, & Sadato, 2008). This structure will be discussed in more detail in the next section as we recorded from this structure to investigate whether inequity modulated activity of striatal neurons.

Inequity encoding and the possible role of the striatum

To summarise this previous chapter, it is well known that many regions in the brain contribute to the circuitry of reward and decision making. In addition there has been growing interest in the neuronal mechanisms of rewards in a social context (Azzi, Sirigu, & Duhamel, 2012; S. W. C. Chang et al., 2013). However, we were particularly interested in the striatum. The striatum is both physiologically and anatomically interesting because it processes both actions and rewards. The striatum has afferents from dopamine cells in the VTA but also receives inputs from the thalamus and cortical areas (Kandel, 2013). From the striatum efferent project to the cortex as well as back to the substantia nigra (Schünke, Ross, Lamperti, Schulte, & Schumacher, 2007). This means that it is an area that is not only important for extra pyramidal movement but also intimately involved with reward processing and decision making (Kandel, 2013). This is supported by fMRI studies as well as extracellular neuronal recordings (Balleine, Delgado, & Hikosaka, 2007; Hollerman et al., 1998; K. Izuma et al., 2008; Kawagoe, Takikawa, & Hikosaka, 1998; Lau & Glimcher, 2007; K. Samejima et al., 2005). Due to its connections to both reward areas and extrapyramidal tracts the striatum processes both actions and rewards which makes it of particular importance for our study into inequity encoding. Social parameters like fairness have also been shown to activate the striatum in some studies (Fliessbach et al., 2007; Tabibnia, Satpute, & Lieberman, 2008). An advantage of the striatum is that its neuronal activity has been relatively well described. In the caudate nucleus of the striatum, 89% of neurons have a very low frequency discharge rate (less than 1Hz). The rest of the neurons fire at 3-8 Hz with quite broad spikes (Hikosaka, Sakamoto, & Usui, 1989a). Slowly discharging cells in caudate and putamen have been said to respond to stimuli of behavioural significance, before and during movements and to preparatory and rewarding stimuli (Alexander, 1987; Crutcher & Delong, 1984a, 1984b; Hikosaka et al., 1989a, 1989b; Liles, 1985; E. T. Rolls, Thorpe, & Maddison, 1983; Schultz & Romo, 1988). Neural activity of ventral striatum has been shown to correlate with the difference in own and other's rewards with equal effort (Fliessbach et al., 2007). Moreover, recent fMRI studies showed that there was a negative correlation between the activity in the ventral striatum and disadvantageous inequity (Fliessbach et al., 2012; Tricomi, Rangel, Camerer, & O'Doherty, 2010).

Importantly, disadvantageous inequity and advantageous inequity may be encoded by neurons in different pathways. This idea is supported by evidence from developmental behavioural studies which show that these phenomena arise at different ages (Blake & McAuliffe, 2011; LoBue et al., 2011). In addition to this, it is also supported by different patterns of correlation between the BOLD signal and the different forms of inequity (Fliessbach et al., 2012). Even though neural results suggest a social component to striatal activity (Fliessbach et al., 2012; Fliessbach et al., 2007;

Harbaugh, Mayr, & Burghart, 2007; Hsu, Anen, & Quartz, 2008; Moll et al., 2006; Tricomi et al., 2010) and reward encoding in striatal neurons has been shown in a variety of studies (Apicella et al., 1992; X. Y. Cai et al., 2011; Cromwell et al., 2005; Cromwell & Schultz, 2003; Hikosaka et al., 1989b; Hollerman et al., 1998; Lau & Glimcher, 2007, 2008; Kazuyuki Samejima et al., 2005; Schultz et al., 1992), not much is known about how single neuron activity is modulated by inequity.

What next?

Inequity and cooperation are extremely important aspects of human social behaviours. Primates also display inequity preferences but the neuronal encoding of this vital information is unknown. The following chapters, will contain the work I performed concerning inequity modulations in striatal neurons (chapter 3). In addition to this I will also look at behaviour toward inequity in a single option task (chapter 2) and a choice task (chapter 4) followed by social choices in coordination (chapter 5) and cooperation (chapter 6). In the next chapter, I will attempt to characterise macaque attitudes towards inequity in an experimental setting.

Chapter 2 – Experiment 1, Part 1: Inequity related behaviour in an imperative giving task

Theories in the fields of economics and biology independently point to inequity aversion as an important factor in decision making in social contexts. In this study rhesus macaques performed a task in which they earned rewards for themselves and another monkey. The reward for self and the other were varied to manipulate the amount of inequity in the reward delivery. Response times and error rates were recorded in this task to study the animals' social preferences. Rigorous analysis of response times failed to answer whether the animals have social preferences. Because the exact nature of the behavioural response depended on the amount of reward for the actor it was hard to pinpoint a particular inequity preference. However what did become clear is that rhesus macaques perceived inequity and responded differently with varying levels of inequity. This conclusion validates this task as one in which inequity is a parameter that can be studied in neuronal activity.

Note: This project as described in chapters 2 and 3 has been published as “A neuronal reward inequity signal in primate striatum” in the Journal of Neurophysiology (Báez-Mendoza, van Coeverden, & Schultz, 2015). I worked closely with Raymundo Báez-Mendoza on this project in which he taught me how to record neurons in primates. The content of this chapter will focus more strongly on the parts of the project that I was involved in. The contents of this and the next chapter therefore overlap with the publication. In some places I have chosen to perform the analysis in a slightly different way and I have added more behavioural results to make the observations of behaviour in the task more informative. The neuronal results are identical to those in the paper as they do not lend themselves to any alternative interpretation or variation of analysis.

Aim

Inequity is important for decision making in both human and non-human primates. With this experiment we aimed to find out whether inequity modulated response times and error rates in a task in which they had to award rewards to both self and another monkey. As we aimed to study how inequity is encoded in neuronal activity in striatum it was first important to validate the behavioural task as a suitable task to study inequity as a parameter. As social preferences in macaques are not a very well understood yet, I also attempted to try and grasp the social preferences of the tested macaques.

Methods

Animals & Ethics

Two adult male macaques (*Macaca Mulatta*) were trained to use a touchscreen to obtain rewards for themselves and another macaque. The animals were housed together with other adult males in large enclosures with enrichment that was changed every month. A third adult male macaque was also trained to receive rewards in the setup passively. This third macaque was housed in a different room with two adult male macaques. All procedures were approved by the United Kingdom Home Office under the Animals Scientific Procedures Act of 1986.

Setup and Task Design

Two macaques were situated across from one another. A touchscreen, positioned on a table in between the monkeys, was used to perform the task. The monkeys could not reach each other but could see each other and shared the use of the touchscreen which they took turns to use. Before and in between the trials the animals held separate touch sensitive keys which were meant to record the exact start of their movements and to make sure the animals' hand was in the starting position in the centre of the screen and static before a new trial started. The passive, receiving, monkey would not be required to do anything except face forward and not display any disruptive behaviour. Rewards consisted of 0.2ml of Blackcurrant squash diluted 1:10 in water (Ribena, GlaxoSmithKline).

We manipulated inequity in three different designs. These designs varied both in the exact amounts of juice drops offered for self and other and the stimuli that were used. The first of these designs is the only design in which both animals were tested. In this first design, the stimuli consisted of rings and rectangles. The rings indicated drops of juice of which the colour indicated the identity of the monkey for which the juice drops were intended for. Each monkey had their own colour. This meant that both monkeys, even when not performing the task could predict how much juice they would receive from looking at the screen. In this first design monkeys received either a reward or no reward (figure 2.1 C, left). Data in this design was recorded in both Monkey A and B. We then went on to test Monkey B together with another monkey (C). Monkey C was passive and never performed this task. While recording with this pair we made a number of changes to the design to make it into a parametric variation in inequity rather than a variation between reward and no-reward (figure 2.1 C, right). The reason for this was to improve the method and design it specifically to test inequity. In a third and final version of the task we improved the task further by changing the stimuli to make sure that the animals did not show a behavioural response to the varying stimulus sizes and, if possible, eliminate some of the noise in the response time data. Instead of rings and rectangles we used rectangular value-bars (Fig. 2.1 D). In these bars we plotted coloured lines to indicate how much

juice each monkey would receive. All the parametric variations of own and other reward from the second and third designs are shown in figure 2.1 C. The parametric designs were important because our recordings in these designs show that inequity modulation is not an all-or-nothing response but can also be found with smaller, more subtle, levels of inequity.

Figure 2.1- Imperative reward giving task

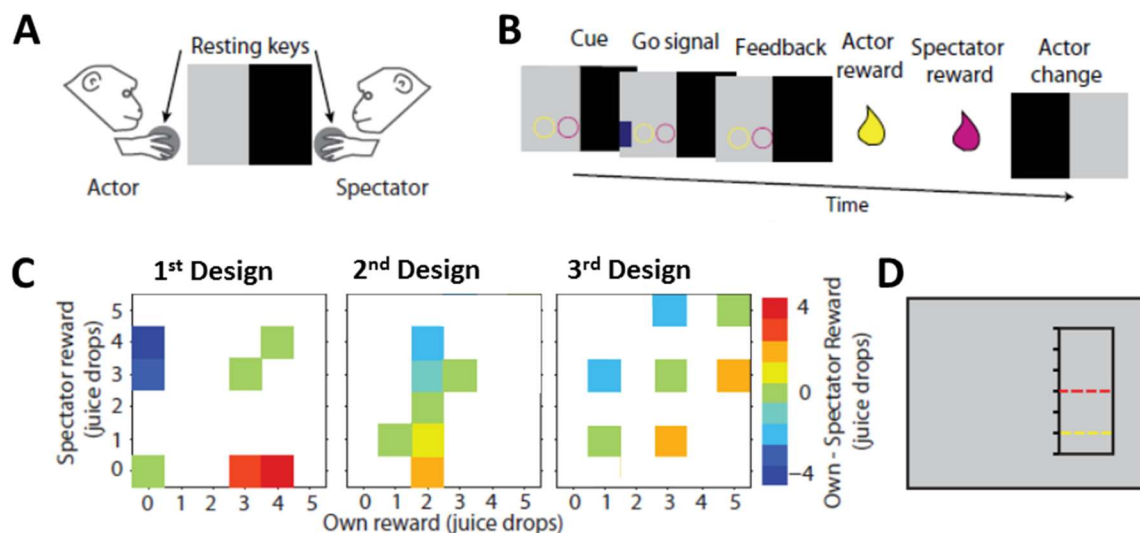


Figure 2.1 (adapted from figure in Báez-Mendoza et al. 2015) General task design and reward conditions. (A) The experimental setup contained a touchscreen at which the two monkeys would sit on opposite sides. Both monkeys also had a touch key to rest their hand on. At the start of each trial a grey background would indicate which animal was the actor on this trial. (B) Task sequence: Stimuli contained circles and squares to predict the reward outcome. After a short delay the target (a small square on the edge of the screen) would light up. This would be the area of the screen that the animal should touch to perform the task. If the animal touched the target area, both animals would receive their respective rewards and the roles would reverse on the next trial. (C) The task designs we used varied over time because we wanted to include various sources of inequity. Designs 1 and 2 used the rings and rectangles depicted in B, the third design used a different type of stimulus. (D) In later versions of our task we controlled for variability in response times due to differences in stimulus sizes by designing value bars that did not differ in size or luminosity. The rest of the task was kept the same. In this specific example stimulus there would be one drop of juice for own reward (yellow) and three drops of juice for the other (red).

Some of the response time analyses I did were solely on the third version of the experiment as the response times contained less noise (due to the design having less visual variability in the stimuli) and I also recorded additional behavioural data in this task which made it a more powerful tool to look at the behavioural results. There was another important change to this last design. The last design contained a balanced amount of variation in own and other's rewards. In the previous parametric design we varied the other's reward more than own reward and therefore any inequity

was always due to a fluctuation in other's reward. In the design with the value-bars this was not the case (figure 2.1 C). By changing the design of our experiment twice we ended up with three alternative designs that all captured inequity in slightly different ways. What we gained from this was that our results were not likely to be specific to one particular design.

Controls – Bucket Control

To compare social behaviour with a non-social control we replaced the passive monkey with a bucket in a subset of the sessions. Regrettably we did not manage to gather enough data in neuronal recording sessions but we have a substantial amount of behavioural data from Monkey B.

Behavioural Analyses

Regression analyses were done to establish whether animals showed a behavioural response in reaction to varying inequity. Only the key parts of the behavioural analysis were used in the published work (Báez-Mendoza et al., 2015) because these analyses were possible in both animals and across all designs. In this way, we could pool all the data and summarise the results, only using the behaviour from the actual neuronal recording sessions. Response times consisted of the time between the onset of the target stimuli and the touch on the screen within the target limits. For behavioural analyses, we used the Fehr and Schmidt model (equation 2.1, discussed earlier in chapter 1) to run regression analyses on response times and error rates.

$$Y = \beta_0 + \beta_1 * W + \beta_2 * \max(Z - W, 0) + \beta_3 * \max(W - Z, 0) + \varepsilon \quad (\text{Equation 2.1})$$

In this equation W and Z are own reward and other's reward respectively. Both of these are expressed in juice drops. Variance inflation factors were calculated to check for correlations of regression coefficients. The variance inflation factors were <2.070 for the non-parametric and <2.092 for the parametric tasks, confirming low inter correlations between regression coefficients. VIF's of higher than 2.5 would be regarded as too inter-correlated which would give a high risk of missing effects by one regression coefficient due to the variance already being explained by another inter-correlated regression coefficient.

To compare regression coefficients of the designs with different magnitudes we multiplied the regression coefficient by the ratio of the standard deviation of the independent variable (own reward or inequity) divided by the standard deviation of the dependent variable (response time or neuronal firing rate) resulting in standardized regression coefficients (X. Cai, S. Kim, & D. Lee, 2011).

In this chapter I will also present response times of the latest version of the task that we used separately and look at additional behavioural sessions that were gathered but not used for the paper. I chose to use this particular part of the data because of the way we conducted this part of the data collection. By only using this part of the data I could separate out conditions and show what the more specific differences between these conditions were.

For the analysis of this data I took the inverse transformation of the response time which transformed it to a normal distribution. As there was less data in this smaller subset it was more important to be prudent about this here. All statistical tests were two tailed. Most of the statistical tests were performed in MATLAB (Mathworks Inc.) except for the secondary analyses performed on the separate behaviour in the parametric design, this was done in SPSS (IBM) by use of univariate ANOVA's.

Data collection, merging of data from projects and the division of roles

Some of the data was recorded in a design that was originally intended to study agency in social interactions (Báez-Mendoza et al., 2013) (Figure 2.1 C, left). This initial data was recorded by Raymundo Báez-Mendoza who also designed this initial task. In the project on inequity coding, I learned how to record neurons from the striatum in the first months. Following this, I recorded a part of the data which was merged with earlier data from the agency project to form our current dataset to study modulation of neuronal activity by inequity. An advantage of using the earlier data in conjunction with new data is that the new data serves as a confirmation that a more parametric modulation still allows us to spot inequity modulation in neuronal activity but allows us to use the earlier data to make a complete picture and extract more information from this data. Considering animal welfare this merging of data is also a way to reduce the amount of experimentation on the animals while still trying to maintain the necessary quality control for drawing conclusions about our data. The difference between the earlier design and later designs is that the later designs contain a parametric modulation of inequity (2nd and 3rd design, figure 2.1 C, middle and right).

Results

Effect of reward and presence of conspecific on response times

Before analysing the dataset from the second monkey for more specific effects of inequity it is important to first look at more simple general effects of own reward and the social context on response times. There was a significant effect of the presence of a conspecific on the mean response time in the task (Variance is equal: $F=.745$ $p=0.388$; Two sample t-test equal variance, $t=4.4$, $p=0.000010$) (Figure 2.2). Because there was a difference in response time with presence of the

conspecific, I first analysed whether own reward explained a significant amount of variance. To check whether animals showed a behavioural change in response times with changes in own reward I used a univariate ANOVA. Both with and without a conspecific present, there was a significant amount of variance explained by own reward (Without conspecific: $F(2,2452)=15.3$, $p=2.5E-7$; with conspecific: $F(2,9449)=32.3$, $p=1.0E-14$).

Figure 2.2 – General effect of conspecific presence on response times

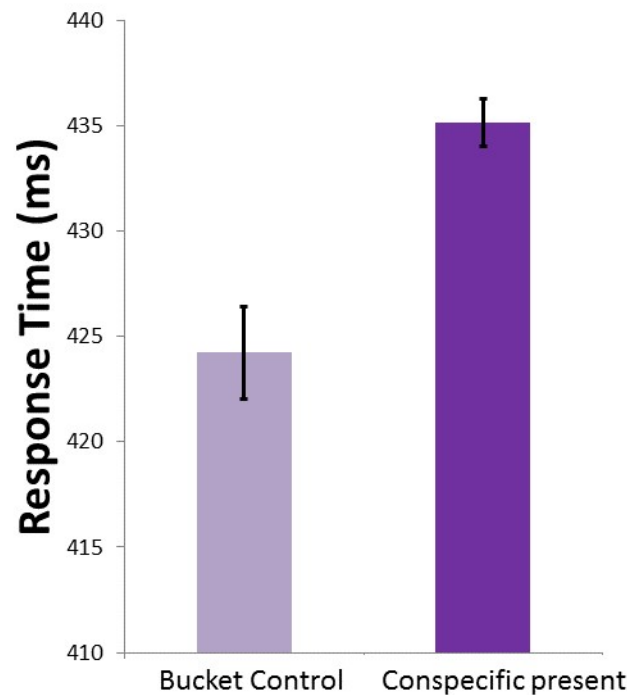


Figure 2.2 Conspecifics presence is paired with an increase in a general increase response times. Animals respond slower when there is another animal present. Errorbars are SEMs. Difference was significant ($p=0.000010$).

When the presence of the other animal was added as a variable into a two way ANOVA, both own reward and the conspecifics presence explained significant amounts of variance in response times (Own reward: $F(2,11901)=34.7$, $p=9.8E-16$; Conspecific presence: $F(1,11901)=21.8$, $p=0.3E-5$). In addition to this, there was a significant interaction between these two effects that was multiplicative in nature when looking at the general pattern. To study this effect the estimated means are plotted in figure 2.3. When the conspecific is present, there is almost no increase in speed with a reward larger than 3 juice drops. With no conspecific present the response times are shorter overall but also keep decreasing with larger rewards over the whole range.

Both own reward and the presence of the conspecific have an effect on response times. It is therefore important for the next analyses to make sure own reward is included in modelling the effects of inequity. Also we look at relative effects of inequity conditions on response times and study the effects separately for conditions with or without a conspecific present.

Figure 2.3 – Effects of own reward and conspecific presence on response times

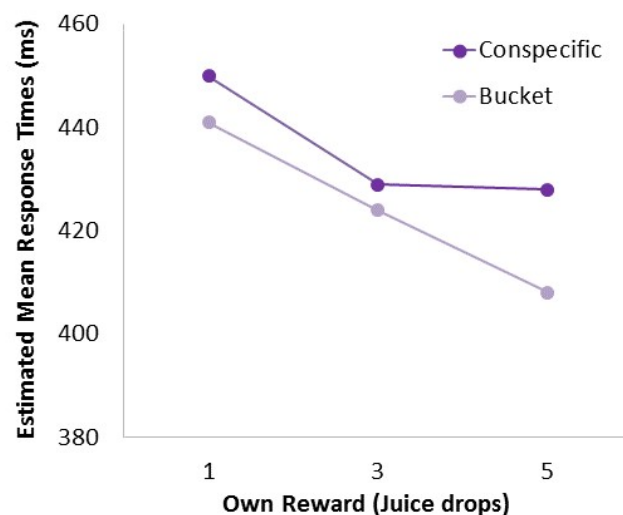


Figure 2.3 Effects of own reward and conspecific presence on response times. There is a multiplicative interaction between the absence of a conspecific and the effect of own reward magnitude on response times. This results in an almost linear relationship between own reward and response times in the bucket control where this relationship has a different shape and slope when the task is performed with a conspecific.

Behavioural responses to inequity

The next step was to investigate whether there was an effect of inequity on response times. I used a linear regression with own reward and the two types of inequity (equation 1) to the response times of all trial blocks that were recorded in the neuronal recording sessions. Results from the general model showed that a significant amount of variance was explained in both animals (Animal A: $F(3,450)=9.35$, $p=5E-6$, adj. $R^2=0.052$; Animal B: $F(3,1271) = 47.45$, $p= 4E-29$, adj. $R^2 = 0.099$).

Example sessions of different designs are displayed in figure 2.4, these illustrate the consistency of the effects across different designs. Increases in own reward magnitude correspond to a significant decrease in response times in both monkeys (figure 2.4, C&D, white bars) as was also shown before in means of a separate behavioural dataset of Monkey B (figure 2.3). Inequity only affected response times significantly in monkey B (figure 2.4, B&D), however response times in monkey A (figure 2.4, A&C) are in the same direction as monkey B (figure 2.4, B&D) (Advantageous inequity: Animal A:

$t(450) = -0.943$, $p = 0.34$; animal B: $t(1271) = -3.79$, $p = 0.0001$; Disadvantageous inequity: Animal A: $t(450) = 1.05$, $p = 0.29$; animal B: $t(1271) = 4.12$, $p = 0.00003$). As can be seen from the example data from a session with the bucket, Animal B (Figure 2.4 E & F), although responsive to inequity in sessions with a conspecific this monkey does not display this same behaviour when performing the task without a conspecific present.

Figure 2.4 – Example response times, Behavioural data from neuronal recording sessions

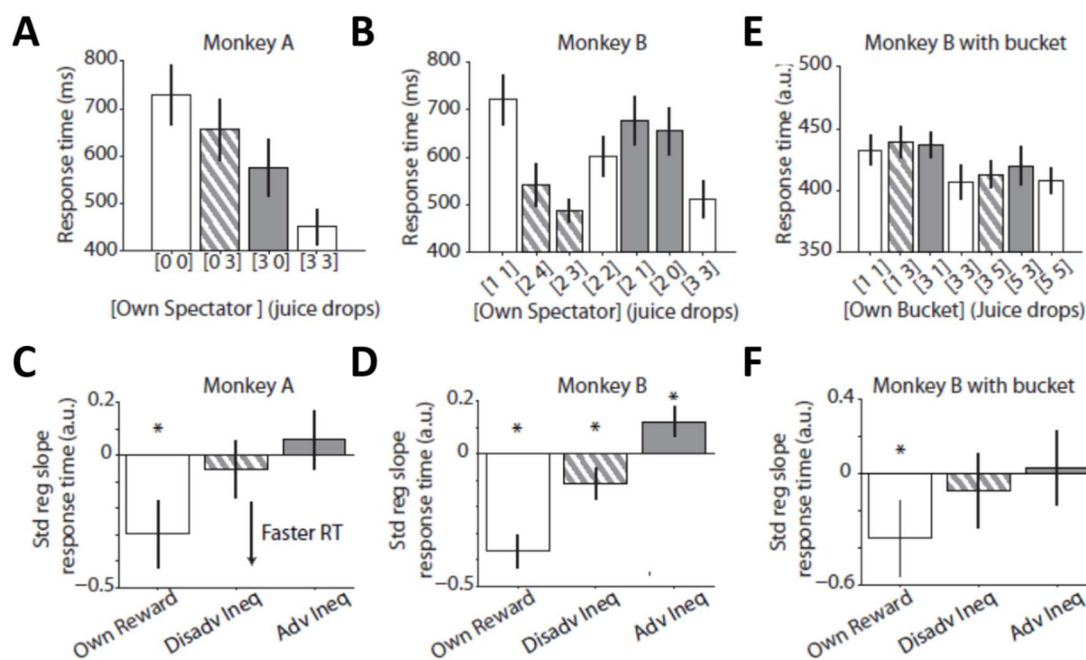


Figure 2.4 (published in Báez-Mendoza et al. 2015) Displays the behavioural data as was recorded in neuronal recordings described in chapter 3 (A&B) Mean response times for different reward conditions from one experimental trial block completed by monkey A (A), monkey B (B). In A&B, monkeys performed the task with a conspecific as spectator, and in E monkey B performed the task with a bucket as a “spectator” as can be seen the effect of inequity seen with a conspecific is not seen in sessions with a bucket in this animal. Error bars show mean \pm SEM. (C,D,F) Standardized regression slopes (Std reg slope) for each regressor from the reward inequity model (Eq. 1) fit to block mean response times from all experimental trial blocks. Bars show 95% confidence intervals. White: own reward; diagonal stripes: disadvantageous inequity; grey: advantageous inequity. An asterisk denotes $p < 0.05$. Monkey A (D) and monkey B (E-F). Data in A-D were recorded in neuronal inequity test trials.

We also quantified the effect of own reward and reward inequity on error rates. The animals committed an error if they did not touch the resting key at the start of their trial, or if they released the resting key before the onset of the go signal, or if they failed to touch the touchscreen once the go signal was shown. The acting animal had to repeat the same trial type until completed correctly. Both monkeys made less errors if they received higher rewards ($t(838) = -4.62$, $p = 4 \times 10^{-6}$, $t(2232) =$

-15.74, $p = 4 \times 10^{-53}$); Monkey A and B respectively, but only monkey B was sensitive to reward inequity. It made less errors with increasing reward inequity in both advantageous and disadvantageous forms ($t(2232) < -3.32$, $p < 0.0008$). These results suggest that response times and error rates in one monkey were sensitive to disadvantageous and advantageous inequity.

To further investigate the nature of the behaviour in response to inequity, I took the response times from a portion of the data that had a design that included equal variation in own and other's reward and performed a three-way ANOVA using the same terms as stated in equation 1, own reward, disadvantageous inequity and advantageous inequity. I did this for data where there was a conspecific present but also for data where the conspecific was replaced with a bucket. In both cases significant variance in response times was explained by own reward (With conspecific: $F(2,9445)=30.1$, $p=9E-14$; With bucket: $F(2,2448)=9.1$, $p=0.0001$). Only in data with a conspecific present I observed a significant amount of variance explained by disadvantageous inequity (With conspecific: $F(1,9445)=5.8$, $p=0.016$; With bucket: $F(1,2448)=0.006$, $p=0.9$). Neither in the condition with a conspecific present, nor with a bucket to receive rewards was an effect of advantageous inequity observed in this analysis.

Figure 2.5 – Response times, behavioural data from third design

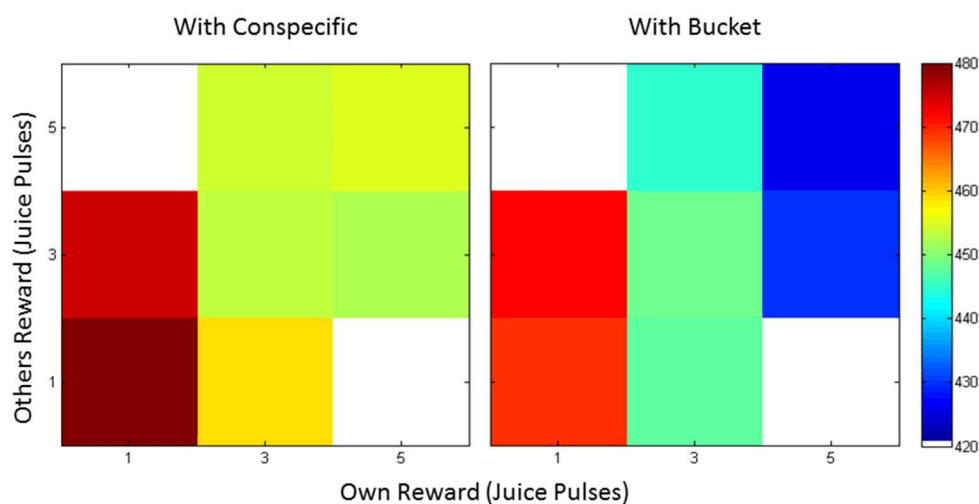


Figure 2.5 Response times, behavioural data from the third design When comparing the two heat maps it is clear that response times are generally lower with a bucket for all conditions. Even so for higher rewards in the context with a conspecific response times seem to not go below 452ms. Comparisons between neighbouring conditions show that in the context with a bucket all comparisons with varying own rewards are significant, however all comparisons with varying others' reward or inequity are not. With another animal present even though there is an overall effect of inequity, in this side by side comparison the main effect seems to be located in the conditions where the acting monkey receives one drop of juice.

It should be noted that a significant interaction was also observed between own reward and disadvantageous inequity, but not in the condition without a conspecific. As the interaction is one with non-crossing lines, the main effects should still hold true, only the actual effect sizes are hard to interpret.

To facilitate an interpretation of effects of inequity on response times, I performed two-sample t-tests to determine which neighbouring conditions were significantly different from each other (figure 2.5). When there is no conspecific present none of the comparisons where own reward is kept equal are significant (P range=0.57-0.87), whereas comparisons where other's reward is kept equal show that an increase in own reward consistently affects response times (P range=0.002-0.014, three out of four results are below Bonferroni significance threshold <0.0125). When we contrast this against the results in the sessions with a conspecific present a very different pattern emerges. In fact, only when own reward is one juice drop is there a significant difference in response times ($p=0.005$, (Bonferroni significance threshold <0.0125)) with change in other's reward. Significant differences in response times were also observed with an increase of own reward from one drop to three drops ($P<0.0001$, (Bonferroni significance threshold <0.0125)). However no significant difference was observed in comparisons where the reward for self or other was larger than 3 juice drops.

To verify whether these more specific comparisons are recognisable in the more parsimonious general model used for the ANOVA I plotted the estimated means from a model in which the animal presence was added as an additional variable and inequity was calculated as the absolute value of inequity (figure 2.6). This model is not used for any other results because disadvantageous and advantageous inequity encoding are possibly caused by different mechanisms, but this was done purely to attempt to separate out inequity in general. When viewing the mean estimates from the ANOVA model we see a similar pattern emerging. This strengthens that it is indeed a good fit with the data shown in figure 2.5. Something that is illustrated by comparing the first two columns of figure 2.6 is the difference between the interaction terms in the models. With no other animal present there is an increased inverse response time (thus, a decrease in 'response time') independent of inequity, however when another animal is present there is an interaction between the effects of inequity and reward on response times.

Figure 2.6 – Visual assessment of ANOVA results to compare with post hoc results

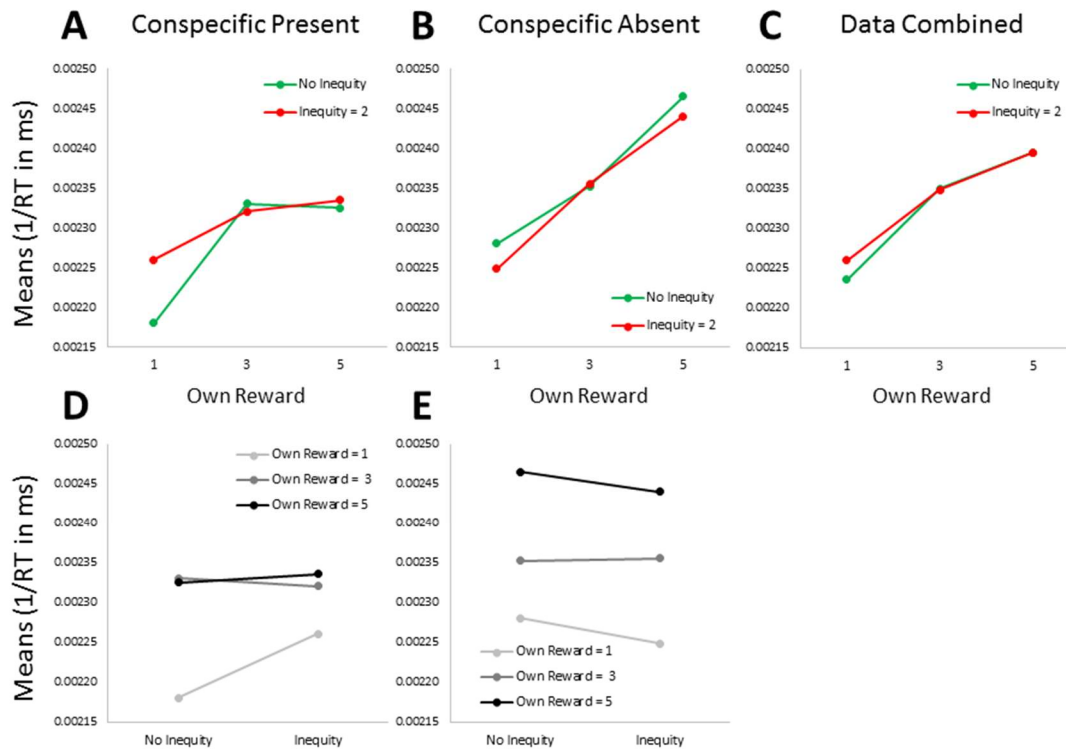


Figure 2.6 Mean estimates from ANOVA model show clear relationship between own reward and inequity. When comparing social with non-social context this relationship is less straightforward. The largest effect of inequity can be seen in the context with a small reward for self. This is true for both social and non-social contexts. However, in the non-social context inequity does not explain a significant amount of variance.

Conclusions

With this experiment we aimed to find out whether macaques show inequity related preferences in response times. First the effects of own reward and the presence of the conspecific were analysed. It is clear that both own reward and the conspecific's presence have an effect on response times of the acting animal. When adding both of these factors into one model, there is a significant interaction effect of these two factors. When studying the estimated means of this analysis is clear that the presence of the conspecific decreases the effect size of reward on response times. Both the presence of own reward magnitude and the social context of the task affect response times in monkeys.

Next we can conclude that inequity had an effect on behaviour in only one of the animals. Even though only one of the animals shows a significant difference in behaviour in response to inequity, the other animal's more subtle differences in response times are in the same direction. When

contrasting Monkey B's effects of inequity with those recorded with a bucket, this shows that these changes in response times are subject to the social context in which they were recorded. To further investigate the effects of inequity on response times, a separate portion of data from monkey B was analysed in further detail. This portion of the data also confirmed what was already described before. There was an effect of own reward both with a bucket and a conspecific receiving juice. However the effects of the other's reward were only seen in the context when there was a conspecific present. Separate comparisons between neighbouring conditions showed that the two means that showed the biggest difference in response time related to a difference in inequity occurred when the reward for the monkey himself was small (1 drop). In addition to these main effects it should be noted that there was an interaction between effects of inequity and own reward on response times, again, only when there was a conspecific present.

The behavioural results do not suggest a clear and consistent attitude towards inequity in macaques. However it is clear that at least one of the animals showed a significant behavioural response to inequity which means that this parameter was taken into account and is likely to somehow have modulated neuronal activity.

Discussion

Presence of conspecific affects the response to reward stimuli

Response times were significantly slower with another animal present. In this contrast the same design was used in both datasets with the same amount of reward, the only difference was the presence of either a conspecific or the presence of a bucket in which the rewards for the 'other' are dropped. Which aspects of the presence of the conspecific causes this increase in response times is unclear. It is likely that the other animal is a distraction causing a slight increase in response times through interference. However, if this were the only factor, you would expect this to be a constant factor regardless of the effect of own reward. This was not the case, there was a decrease in the effect of reward on response times which could possibly mean that the animals are less sensitive to the reward stimuli if another animal is present. Because later analysis shows a sensitivity to inequity, possibly the presence of inequity in a social context distracts the attention away from own rewards.

Inequity behaviour depends on social context

The animals' response times were shorter with increasing own rewards, this confirmed earlier findings (Watanabe et al., 2001). In both animals the reaction times decreased with advantageous inequity and increased with disadvantageous inequity. This change was only statistically significant in one animal. Our behavioural results confirm earlier findings that macaques are sensitive to rewards

of others (Azzi et al., 2012; Steve W. C. Chang, Winecoff, & Platt, 2011). One could wonder whether the animal in which there was no significant behavioural effect of inequity was sensitive to reward inequity at all. With the body of evidence that suggests that macaques are sensitive to reward inequity (S. Brosnan, 2006; Sarah F Brosnan, 2009; Sarah F. Brosnan & de Waal, 2003; Massen, Van Den Berg, Spruijt, & Sterck, 2012; van Wolkenten, Brosnan, & de Waal, 2007) that seems unlikely. This chapter also showed some (albeit limited) evidence that inequity preferences are dependent on the social context (with monkey vs. with bucket) and it is possible that if this monkey was paired with a different conspecific that he would respond differently. The social control task we performed with one of the monkeys suggested that the behavioural effect of inequity was dependent on the social context of the task. However, the behavioural results do not suggest a defined relationship between inequity and value for primates as it has been known to influence value in humans (E. Fehr & Schmidt, 1999; Loewenstein et al., 1989). Possibly reciprocity is also an important factor. Our parametric design in which only one monkey was the actor allowed us to remove effort as a source of variation. However, one can wonder whether we removed an important part of the social context which may have been needed to establish stronger social preferences. Nevertheless, even with only a passive conspecific the effect of inequity on behaviour was dependent on the social context, as could be seen by the lack of an effect in the 'bucket' control task.

The necessity of a social context does not necessarily mean that the behaviour can only be explained by motives of social preferences. Motives of social preferences are for example, caring about another's reward or having preferences for equal rewards. Slower reaction times in disadvantageous inequity could alternatively be the result of fear of reprisal by the dominant monkey. Another example is that a faster response time in disadvantageous inequity could be the result of a desire to get to the next trial quicker. Other experiments would be needed to comment on the underlying motives of the monkeys.

Social dominance and inequity related behaviours

Macaques live in very strict social dominance hierarchies (Maestripieri, 2007). There could be an effect of social dominance on the tolerance or sensitivity to inequity. Our experiments cannot answer questions on social dominance as we only tested two animals. We can however add that Monkey A was socially dominant over monkey B. Perhaps dominant monkeys in these particular circumstances are less sensitive to inequity which would account for the lack of a behavioural response in Monkey A.

Chapter 3 – Experiment 1, Part 2: The encoding of inequity in the striatum

Inequity aversion is an important social factor in decision making. Activity in the striatum has been found to correlate to various social factors including inequity (see chapter 1). We recorded neurons in the striatum of Rhesus macaques while they performed a task in which they earned rewards for themselves and another monkey. Behavioural analysis in the task has been described in the previous chapter (chapter 2). It showed that although social preferences vary in macaques, animals do change their behaviour with varying levels of inequity. This means that the animals both perceive and have a behavioural response to inequity. The aim of the neuronal recordings was to research how striatal activity in macaques varies with inequity. The amount of reward for self and other were varied to manipulate the amount of inequity in the reward delivery. We tested whether neurons in the striatum responded to varying amounts of inequity. We classified neurons as coding own reward, disadvantageous or advantageous inequity based on a regression of their task related responses to a model incorporating these three terms. We found that of the 345 neurons that we recorded 32% was modulated by reward inequity in at least one task related response. This is the first ever account of reward inequity encoding in striatal neurons.

Aim

Inequity is important for decision making in both human and non-human primates. Activity in the striatum has been found to correlate to various social factors including inequity (see chapter 1). However, little is known about how single neurons in the striatum encode inequity. Knowledge about how the brain processes social information could potentially contribute to a better understanding of how the reward system contributes to social behaviour. With this experiment we aimed to find out whether inequity modulates neuronal activity in striatal neurons.

Methods

Animals & Ethics

Two adult male macaques (*Macaca Mulatta*) were trained to use a touchscreen to obtain rewards as described in the previous chapter. These animals were implanted with metal chambers by means surgeries under isoflurane anaesthesia. The chambers allowed us to head-fix the animals and gain access to the brain through a craniotomy. A third adult male macaque was also trained to receive rewards in the setup but this animal was neither implanted with a chamber nor used for neuronal recordings. This third macaque was housed in a different room with two adult male macaques. All

the experimental procedures were approved by the United Kingdom Home Office under the Animals Scientific Procedures Act of 1986.

Setup and Task Design

Setup and task design are described in detail in chapter 2. In summary, two animals were seated across from each other and were trained to do an instrumental task in which they touched a target on a touchscreen to obtain rewards for themselves and a conspecific. We varied the rewards for self and other with the aim to vary the amount of inequity between the rewards while keeping other factors constant. Behavioural analyses show that the animals display a varying behavioural response to inequity.

Neuronal recordings

We recorded extracellular activity from single neurons in the striatum. The location of the striatum was determined using previously mapped coordinates of this area. We recorded contralateral to the moving arm, from the striatum, anterior to the anterior commissure. In the task in which there was only reward or no reward delivered to self or other, we recorded from 56 sparsely discharging neurons in monkey A and 96 neurons in monkey B. In a later parametric version of the task in which only one monkey was the actor another 193 neurons were recorded from monkey B. I was personally only involved in these recordings from monkey B and was involved in the recording of a substantial amount of these neurons (the exact amount is hard to determine as we worked together on many of recordings and it would be hard to class those recordings as mine or his). We only recorded from slowly firing neurons. We isolated activity of single neurons online using a window discriminator (DIS-1, Bak Electronics Ltd.), and offline with spike sorting software (Offline Sorter, Plexon Inc). All offline sorting was performed by Dr. Báez-Mendoza.

Neuronal analyses

We did not have a specific epoch in the task that we were interested in as we did not make any assumptions about when inequity would be a factor. Therefore, we analysed neuronal activity in six task epochs of interest. These epochs were all 500ms in length starting from: 250ms after cue onset, target onset, movement feedback (500ms after target onset), 500ms before reward delivery, reward delivery and conspecifics reward delivery. If a task epoch had a significant fit to our model in an epoch we classed this as a significant ‘modulation’ a term which we use to describe the effect of the task on neuronal activity at a specific time.

To analyse whether neuronal activity was related to reward and/or inequity we used the Fehr and Schmidt equation (Eq. 1) for linear regression of the neuronal activity. Only when the entire model showed a significant fit, we tested significance of separate regression coefficients with posthoc t-tests ($\alpha=0.05$).

$$Y = \beta_0 + \beta_1 * W + \beta_2 * \max(Z - W, 0) + \beta_3 * \max(W - Z, 0) + \varepsilon \quad \text{Equation 3.1}$$

Because we didn't want our entire assessment of striatal modulations to hinge on the Fehr and Schmidt model of inequity we also tested the following alternative models:

Total available reward:

$$Y = \beta_0 + \beta_4 * (W + Z) + \varepsilon \quad \text{Equation 3.2}$$

Reward difference between animals:

$$Y = \beta_0 + \beta_5 * (W - Z) + \varepsilon \quad \text{Equation 3.3}$$

Conspecific's reward magnitude:

$$Y = \beta_0 + \beta_6 * Z + \varepsilon \quad \text{Equation 3.4}$$

Linear combination of own reward magnitude and conspecific's reward magnitude:

$$Y = \beta_0 + \beta_1 W + \beta_6 Z + \varepsilon \quad \text{Equation 3.5}$$

We used the Akaike Information Criterion (AIC) to identify the best fit between all of these models. The AIC is a measure of the fit of models and provides a measure of the relative strength of evidence for each model given a set of models. It is a good measure compared to for instance a simple comparison of r-squares because it takes the amount of parameters in the model into account. Another method to do this is the Bayesian Information criterion (BIC), however the BIC was designed to find the true model and therefore penalizes models for containing free parameters more. The AIC was designed to find the model that fits the data best, assuming that the 'real' model is not amongst the models tested. Based on this the AIC is the more appropriate choice for our intended purpose. When using the AIC, the model with the smallest numerical outcome has the best and most parsimonious (trade-off between model fit and least amount of parameters) fit to the data (Lewandowsky & Farrell, 2011). The equation to calculate the AIC is:

$$AIC = n * \log\left(\frac{SSE}{n}\right) + 2k \quad \text{Equation 3.6}$$

SSE is the sum of squared errors, n is the number of recorded trials and k is the number of independent variables (including the intercept).

Histology

Both animals were euthanized with sodium pentobarbital (90mg/kg, intravenous) and subsequently perfused with 4% paraformaldehyde in 0.1M phosphate buffer. Marking pins were placed at the boundaries of the coordinates of neuronal recordings. From this, recording positions were reconstructed from 50 μ m cresyl violet stained coronal sections to confirm the locations of electrode placement.

Results

Overview

We studied the activity of 347 sparsely firing neurons in the anterior striatum of two monkeys. The data will be described separately for the first design in which 152 neurons (monkey A: $n=56$ neurons, monkey B: $n=96$) were tested and the second and third designs in which an additional 193 neurons were tested. Of 152 neurons, tested in the first design, 84 (55%) showed reward related activity modulations during one of several task epochs (186 reward-related activity modulations). Specifically, 31 neurons showed modulations in 36 epochs reflecting reward inequity without coding the magnitude of the reward to the recorded animal ('own reward'; 11 neurons recorded from monkey A showed 15 modulations), 34 neurons showed modulations in 52 epochs reflecting reward inequity and own reward magnitude (16 neurons recorded from monkey A showed modulations in 34 epochs), and 60 neurons showed modulations in 98 epochs reflecting only own reward magnitude without coding reward inequity (24 neurons recorded from monkey A showed modulations in 40 epochs). We did not find any evidence that there was a difference in the physiological distributions of cells between the animals. The number of neurons in categories was not significantly different between the two monkeys ($\chi^2(2) = 0.93$, $p = 0.62$). Several neurons showed more than one modulation during the different task epochs and thus belonged to more than one category.

In the first design (figure 2.1 C, left) only presence or absence of reward was tested, therefore this assessed only one level of reward inequity and one level of reward magnitude. To obtain more graded assessments of inequity, we used second and third designs with several reward magnitudes and accordingly several inequity levels (Figure 2.1, C (middle and right) & D). This task required only one monkey to act, which provided additional opportunities for testing inequity without the potential influence of effort cost. We only recorded neurons in this task in monkey B. We recorded

an additional 193 neurons in this task. The activity of 90 of 193 tested striatal neurons (47%) showed modulations adhering to one of the three main categories.

Neuronal Modulations by Inequity

The activity of 31 of the 152 striatal neurons in the first design (20%) with modulations in 36 epochs specifically signalled the differences in reward between the two animals without coding own reward magnitude as well. This was defined by the neuron showing a significant fit in the overall regression (Eq. 3.1) and with post hoc significance of either the disadvantageous or the advantageous reward inequity regressor or with both inequity regressors. Activity in all of these neurons showed trends with regards to own reward with no exception. Of the 31 inequity modulated neurons, the activity of 18 neurons with modulations in 22 epochs reflected disadvantageous inequity, without coding own reward (6 neurons, 9 modulations recorded from monkey A). The activity of 12 striatal neurons with neuronal modulations in 13 epochs reflected advantageous inequity (5 neurons, 6 modulations from monkey A). The activity of 1 striatal neuron with a single neuronal modulation reflected disadvantageous and advantageous inequity together (recorded from monkey B). Thus, neuronal modulations reflecting separately disadvantageous or advantageous inequity were more frequently found than modulations coding both inequity forms (35 vs. 1; $p < 0.001$, binomial test).

The activity of 34 of the 152 tested striatal neurons (22%) with modulations in 52 epochs reflected reward inequity and own reward magnitude. Of these 34 striatal neurons, the activity of 17 neurons with modulations in 23 epochs reflected disadvantageous inequity (6 neurons, 13 modulations from monkey A), the activity of 17 neurons with modulations in 24 epochs reflected advantageous inequity (10 neurons, 16 modulations from monkey A), and the activity of 4 striatal neurons with 5 neuronal modulations reflected disadvantageous and advantageous inequity together (all recorded from monkey A). No evidence was found that one type of inequity was more frequently encoded by neurons, as the number of neurons and modulations recorded from each monkey was not significantly different between the two categories of inequity ($\chi^2(5) = 8.712$, $p = 0.12$; $\chi^2(5) = 8.84$, $p = 0.11$, for neurons and modulations, respectively).

Figure 3.1 – Examples of reward inequity coding in reward sensitive striatal neurons

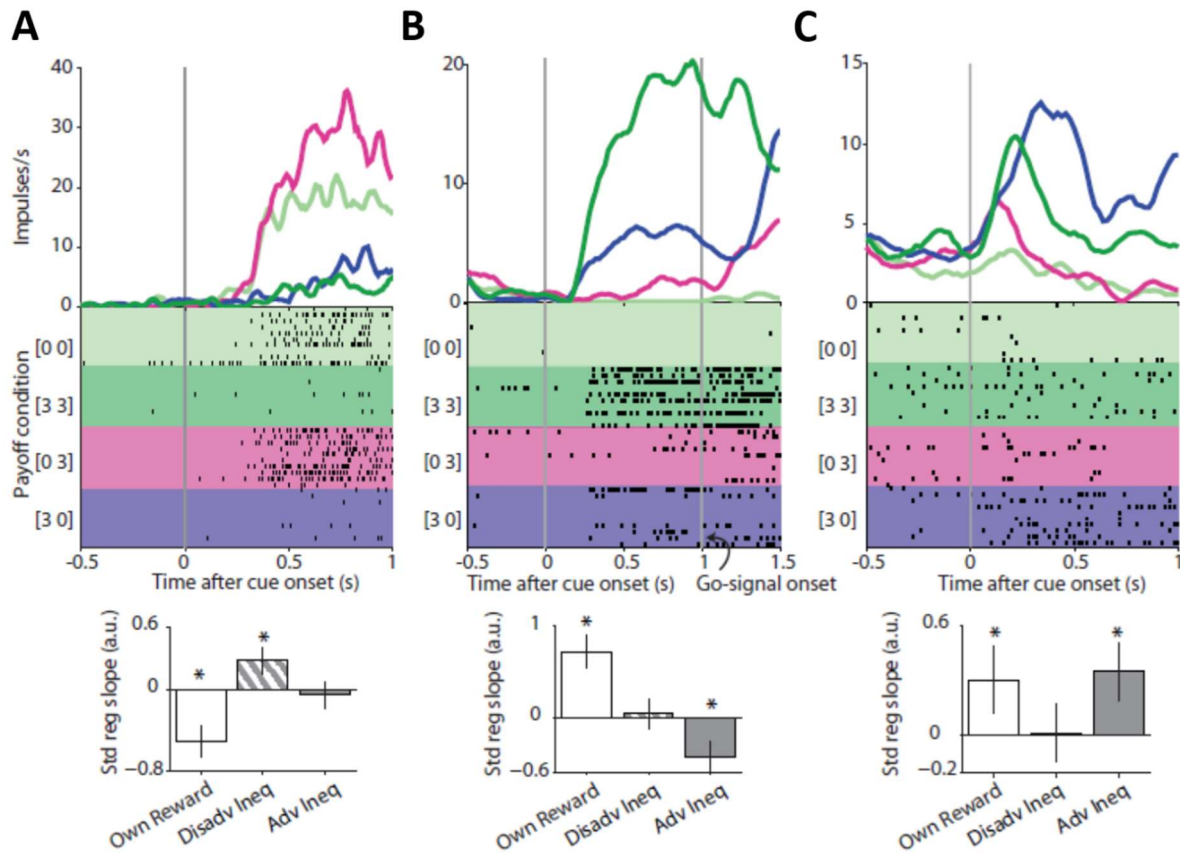


Figure 3.1 (adapted from figure in Báez-Mendoza et al. 2015) Examples of reward inequity coding in reward sensitive striatal neurons. (A) Disadvantageous inequity coding in inverse reward magnitude coding neuron, with non-significant modulation by advantageous inequity (magenta: disadvantageous inequity; blue: advantageous inequity; green on different shades of green: equity). Note the opposite direction between reward magnitude and disadvantageous inequity coding. Monkey A. (B) Advantageous inequity coding in reward magnitude coding neuron. Note opposite direction between reward magnitude and advantageous inequity coding. Monkey A. (C) Advantageous inequity coding in the same direction as reward magnitude coding. No effect of disadvantageous inequity. Monkey A. In A-C, rastergrams include only 10 trials of each condition for clarity, bin size = 20ms. Bottom panels show magnitudes of standardized regression slopes \pm 95% confidence intervals for each regressor (Eq. 1). An asterisk denotes $p < 0.05$.

As mentioned in the previous paragraph, the large majority of reward inequity modulations with own reward coding was sensitive to only one form of inequity, compared to both forms (47 vs. 5). The activity (action potentials/second) of the example neuron shown in Fig. 3.1A decreased with increasing reward magnitude (green) and increased when the recorded animal received less reward than the conspecific (magenta) but it was not modulated when the animal received more reward than the conspecific (blue). As is illustrated in the bar graph, this neuron coded disadvantageous inequity in the opposite direction to own reward magnitude coding. In another example neuron

illustrated in figure 3.1B, activity was lower when the animal received more reward than the other animal (advantageous inequity coding, blue) compared to when both animals received the same reward magnitude (dark green). The activity of the neuron in Fig. 3.1C increased with advantageous inequity (blue) and with increasing reward magnitude (green). Taken together these examples are illustrative of the suggestion that subgroups of neurons in the anterior striatum code specific forms of reward inequity. In addition, reward coding neurons and inequity modulated neurons are not separate but overlapping populations of neurons.

Figure 3.2 – Reward inequity coding in reward sensitive striatal neurons in different conditions

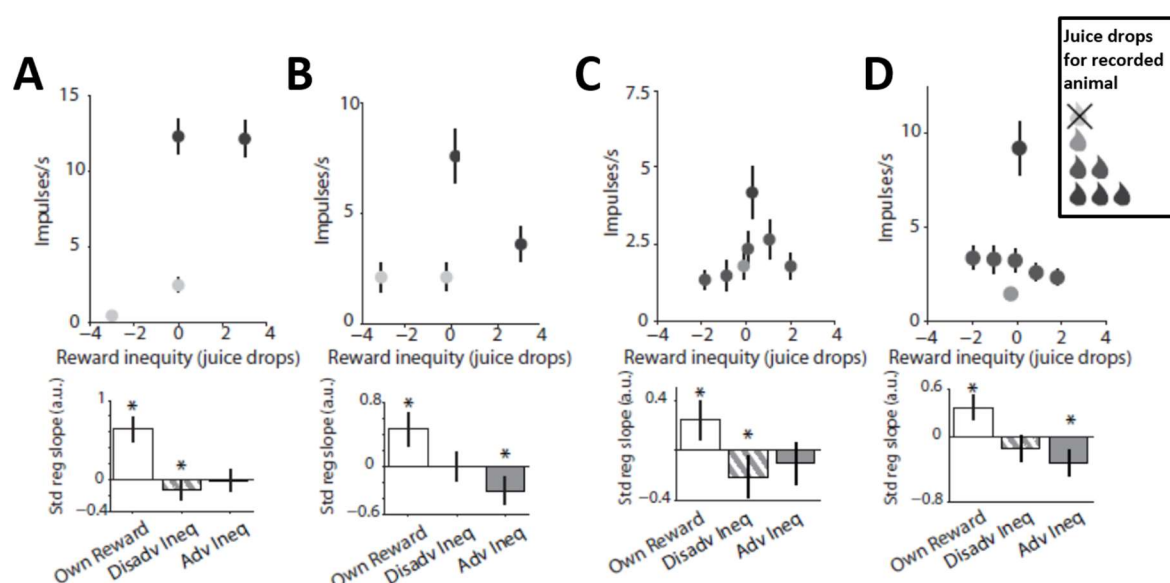


Figure 3.2 (adapted from figure in Baez-Mendoza et al. 2015) Reward inequity coding in reward sensitive striatal neurons in different task conditions. (A, B) Neuronal modulations recorded in the first design of the task showing own reward coding with either: disadvantageous inequity (A) or advantageous inequity (B). Scatter dots show mean neuronal activity in an analysis window. (C, D) Same as A, B, but these neurons were recorded during the second and third designs of the task. In the abscissa, reward inequity is defined as own juice drops minus conspecific's juice drops. Neuronal modulations showing disadvantageous inequity coding show a decrease in activity with negative reward inequity, and those modulations showing advantageous inequity show a decrease in activity with positive reward inequity. Scatter dot black saturation indicates the number of juice drops received by the recorded monkey: lighter grey=0, medium grey=1, dark grey=2, black=3. Error bars are mean \pm SEM. An asterisk denotes $p < 0.05$.

In the latter designs (as previously discussed), the activity of 37 of the 193 neurons (19%) reflected reward inequity, but not own reward magnitude. Of these, 12 neurons with modulations in 15 epochs coded disadvantageous inequity; 17 neurons with modulations in 21 epochs coded advantageous inequity and 9 neurons with modulations in 10 epochs coded both forms of reward

inequity (1 neuron showed advantageous and both forms of inequity coding with different task events). The activity of a smaller amount of neurons (19 neurons, 10%) coded both reward inequity and own reward magnitude. Of these, 7 neurons (8 modulations) coded disadvantageous inequity, 10 neurons (12 modulations) coded advantageous inequity, and 2 neurons (2 modulations) coded both forms of inequity. These results from the second and third designs confirm inequity coding as seen in the first design of the task and provide more quantitative information about inequity coding (Fig. 3.2). In figure 3.2, reward inequity was defined as the difference between own juice drops and the conspecific's juice drops. Thus, negative numbers represent disadvantageous inequity, and positive numbers represent advantageous reward inequity. The activity of 54 of the 193 neurons (28%) with modulations in 65 epochs coded own reward magnitude irrespective of reward inequity. The number of neurons in each category varied non-significantly between the first and later designs ($\chi^2(2) = 4.15, p = 0.12$). Thus, the second and third designs with extended payoff matrix and constant effort cost confirmed all types of reward-related coding found in the first design. As no evidence was found to suggest a difference in the physiological distributions of neurons between animals or designs we saw no reason not to pool the data from all designs to study inequity coding in more detail. In the following analyses, data from all tasks was pooled. The results from the main regression analyses are summarized in Table 3.1.

Table 3.1 – Number of neurons (modulations) coding reward inequity

	Disadvantageous Inequity	Advantageous Inequity	Inequity (Both directions)	Total
Reward	24(32)	27(35)	6(7)	53(74)
No Reward	30(37)	29(34)	10(11)	68(82)
Total	50(69)	53(69)	16(18)	111(156)

Table 3.1 Numbers of single neuronal modulations with at least one significant modulation during one task period. Some neurons showed effects in multiple periods, sometimes coding one form of reward inequity during one period and another form of reward inequity in a different period. Therefore, the number of neurons in subtotal rows and columns may be lower than the sum of neurons in respective individual rows or columns.

Multiple Comparisons testing

To check that the amounts of inequity encoding neurons are not just a result of errors in statistical classification I calculated whether the amount of neurons classified into this category was more than one would expect if they were purely found by statistical errors. The same statistical model was used

to classify each neuron in 6 different epochs. Based on a cumulative binomial distribution where the chance of a significant outcome is 0.05, the chance that a neuron would be found to encode inequity in at least one of the epochs is 0.2649. Based on a binomial distribution with this probability of classification, the probability of finding 111 or more inequity or reward encoding neurons is 0.02. This shows that even when being very conservative the amounts of neurons we find encoding inequity are significantly more than one would expect if based purely on our method of classification (5% error).

Direction of reward inequity coding

The neurons coding reward inequity showed changes in activity (both positive and negative coding) with increasing inequity. This was indicated by positive or negative regression slopes (figure 3.3). Neurons coding inequity irrespective of own reward showed predominantly positive regression slope for inequity (53 modulations with a positive sign out of 71, $p = 0.00004$, binomial test; Fig. 3.3A). Neurons coding reward inequity and own reward magnitude were more likely to be associated with a negative regression slope for inequity (46 modulations with a negative sign out of 67; $p = 0.003$, binomial test; Fig 3.3B). Neurons whose activity coded reward inequity but not reward were more likely to reflect reward inequity with an increase in discharge rate, rather than a decrease as in the reward coding neurons.

Figure 3.3 – Standardized regression slopes of reward inequity coding

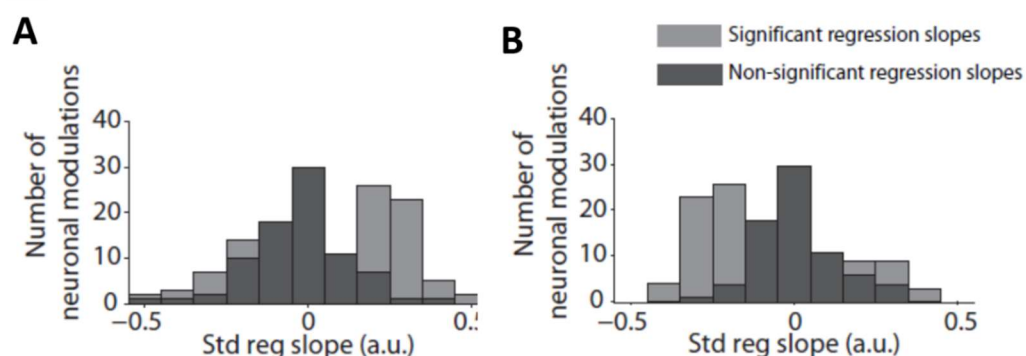


Figure 3.3 (adapted from figure in Báez-Mendoza et al. 2015) Standardized regression slopes of reward inequity coding show different patterns of coding inequity dependant on the coding of reward of the same neurons. (A) Neuronal modulations not coding own reward magnitude. (B) Neuronal modulations coding also own reward magnitude. Grey: significant regression slopes; black: non-significant slopes.

By contrast, neurons coding reward inequity together with own reward magnitude were more likely to be modulated by reward inequity with a decrease in discharge rate, rather than an increase. Thus, the direction of coding (activity increase or decrease) depended on whether the neuron's activity reflected own reward magnitude or not.

Comparisons between inequity and own reward coding

To compare reward inequity coding with own reward coding, the partial R^2 on neurons coding both inequity and own reward magnitude were compared with each other. Regressions of neuronal responses to disadvantageous inequity showed a lower partial R^2 than regressions on own reward magnitude (0.05 ± 0.004 vs. 0.095 ± 0.015 ; mean \pm SEM). Similarly, neuronal coding for advantageous inequity was associated with a lower partial R^2 than for own reward (0.07 ± 0.005 vs. 0.118 ± 0.015 ; mean \pm SEM). Therefore, inequity coding although clearly present in a subset of neurons may be less strongly represented than own reward coding.

To check whether any more in depth analyses or comparisons between reward encoding neurons and inequity encoding neurons would be valid, I also evaluated whether reward encoding and inequity encoding neurons could be seen as encoded in independent neuronal populations. Based on the contingency table divisions of neurons that encoded reward and the neurons that encoded inequity there was no evidence for independent encoding of these two variable as separate populations ($\chi^2 (1) = 0.16$, $p = 0.69$). As a consequence it would be unwise to contrast these two groups of cells as it would be hard to distinguish any differences in these groups of neurons from selection bias created by our statistical sampling method.

Task epoch distribution

Inequity neurons showed consistent modulations during all analysed task epochs in the trials (figure 3.4). Neuronal activity increased (top row) or decreased (bottom) in relation to disadvantageous inequity (left) or advantageous inequity (right). The difference in the number of modulations in each category and each epoch was non-significant ($\chi^2 (12) = 12.55$, $p = 0.4$; figure 3.4). The statistical results suggests that anterior striatal neurons code reward inequity throughout the task rather than in a specific event related epoch.

Figure 3.4 – Distinct reward inequity coding in neuronal population activity

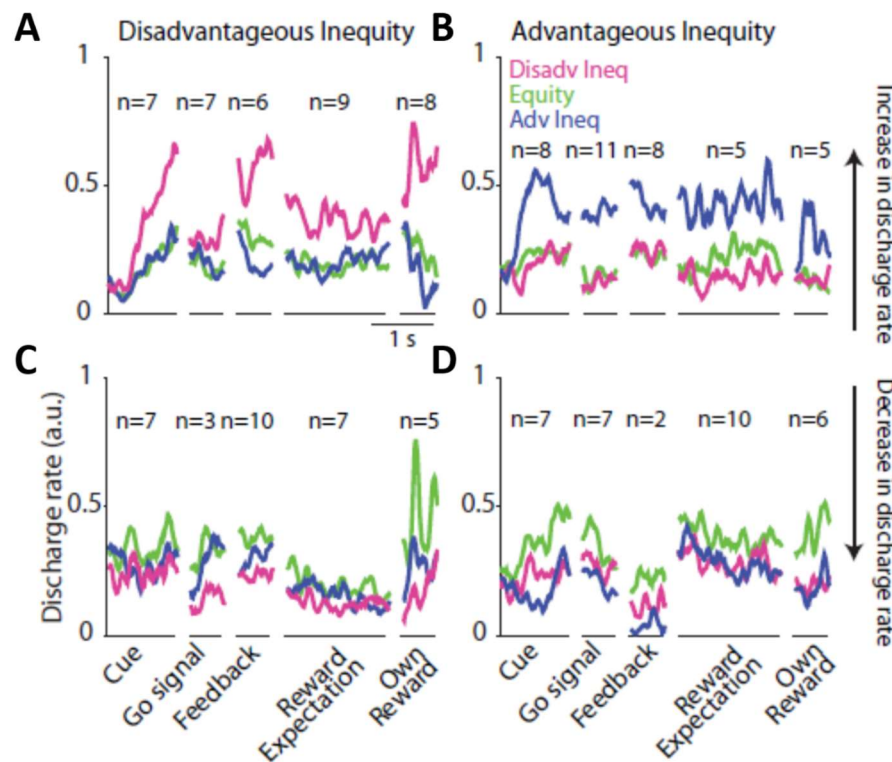


Figure 3.4 (adapted from figure in Baez-Mendoza et al. 2015) Distinct reward inequity coding in neuronal population activity. (A) Normalized spike density function (SDF) of neurons within individual trial epochs showing significantly higher discharge rates with increasing disadvantageous inequity (magenta) compared to equal rewards (green) and advantageous inequity (blue), $n=37$. (B) Population SDF of neurons showing significantly higher discharge rates with increasing advantageous inequity, $n=37$. (C-D) Population SDF of neurons within one trial epoch showing significant decreases in discharge rate with either disadvantageous (C, $n=32$) or advantageous (D, $n=32$) reward inequity.

Alternatives to reward inequity coding

We tested whether variance in neuronal activity reflecting reward inequity might be explained by reward processes unrelated to inequity. To study this we considered four alternative models reflecting alternative hypotheses; these hypotheses were tested with linear regression models (total available reward equation 3.2, reward difference equation 3.3 and conspecific's reward equation 3.4) or with a multiple linear regression (own reward and conspecific's reward equation 3.5). To decide which model best fitted the data, the goodness of fit of all models using the AIC (equation 3.6) was used. The large majority of modulated epochs were best fit by the reward inequity model (126 out of 156, 80%). Of the remaining 30 neuronal modulations, 10 were better fitted by the model with conspecific's reward, 10 better reflected the sum of available reward. Another 10 were better explained by the model with two forms of inequity in opposite directions, which amounted to a continuous coding of reward difference between the recipients and was not considered further.

Not a single neuronal modulation was better fitted by the linear combination of own reward magnitude and conspecific's reward magnitude. Thus, only a small subset of neurons classified as coding reward inequity might have coded other processes associated with rewards.

Anatomical distribution

Figure 3.5 (A & B) shows the location of striatal neurons that coded reward inequity, own reward or both inequity and reward. To investigate whether there was an anatomical difference in the locations of these neurons, we calculated the mean position in all of the coordinates of each class of neurons and estimated a 95% confidence interval with bootstrap test (20,000 iterations).

Figure 3.5 – Neuronal recording locations

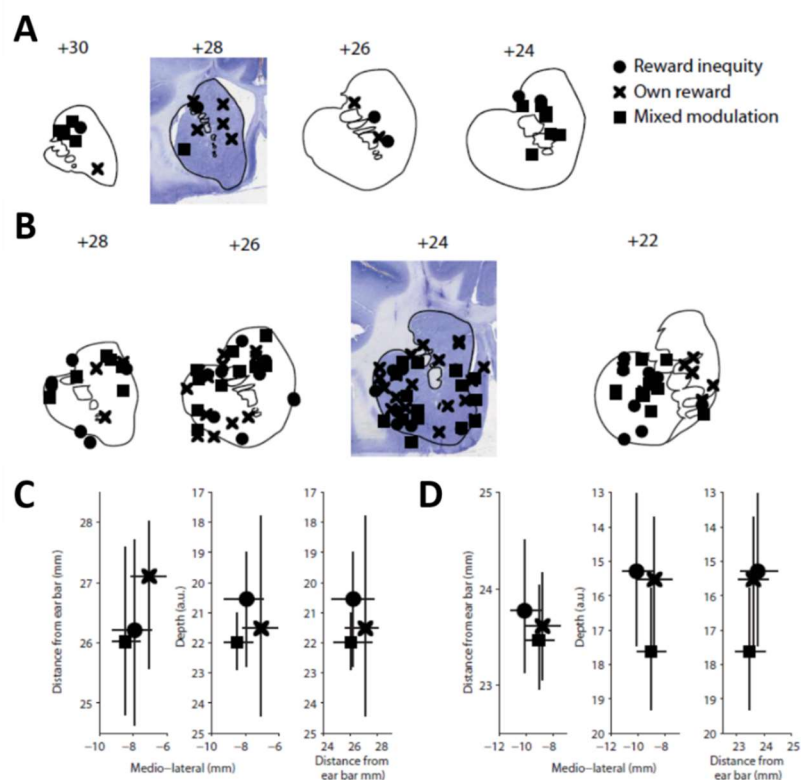


Figure 3.5 (adapted from figure in Báez-Mendoza et al. 2015) Neuronal recording locations. (A) Coronal series showing the recording locations in monkey A for reward-modulated striatal neurons, plotted separately for each neuronal category: modulation by reward inequity (solid circles), by own reward (crosses), and mixed (solid rectangles). Striatum outline was drawn from the Atlas of Saleem and Logothetis (2007). The background in section +28 is a Nissl stained brain coronal slice from monkey A used for recording position reconstruction. (B) Coronal series showing the recording locations in monkey B, conventions as in (A). The background in section +24 is a Nissl stained coronal slice from monkey B. Note gliosis in white matter dorsal to the caudate. (C, D) Centroids (mean position in all coordinate directions) of each class of neurons recorded in Monkey A and Monkey B, respectively. Error bars are 95% CI estimated with bootstrap (20,000 iterations).

If a class of neurons significantly clusters away from other classes its confidence interval should not overlap with that of other classes. We observed that all confidence intervals overlapped from each neuronal class on every dimension (anterior-posterior, medio lateral and depth). This was true in both animals (figure 3.5, C & D). This suggests that, within our sample, striatal neurons modulated by reward inequity, own reward or both did not significantly differ in their anatomical position in the striatum.

Conclusions

By recording neuronal activity from monkey striatum in a task where we varied inequity, we aimed to find out whether inequity modulates neuronal activity in striatal neurons in macaques. After statistical analyses of the neuronal activity we found that a significant proportion (32.2%) of striatal neurons is modulated by reward inequity. Most of these neurons encode either disadvantageous or advantageous inequity rather than both. Only very few encoded both forms of inequity. A much larger amount of the recorded neurons encoded own reward magnitude. The control analyses in which we compared models ruled out that total reward for animals, reward difference, effort cost and eye movements would explain the data better.

Discussion

Inequity behaviour depends on social context

In the previous chapter behavioural results were discussed that were important to the present experiment in which we recorded striatal activity. Some of these results are important to our considerations of the neuronal data. The behavioural results confirm that macaques are sensitive to rewards of others as found in earlier studies (Azzi et al., 2012; Steve W. C. Chang et al., 2011). Both animals response times were shorter with increasing own rewards, this also confirmed earlier results (Watanabe et al., 2001). In both animals the reaction times decreased with advantageous inequity and increased with disadvantageous inequity. Only in one animal this change was significant. We can't confirm with certainty whether the animal in which there was no significant behavioural effect of inequity was sensitive to reward inequity at all. However, with the body of evidence that suggests that macaques are sensitive to reward inequity (S. Brosnan, 2006; Sarah F Brosnan, 2009; Sarah F. Brosnan & de Waal, 2003; Massen et al., 2012; van Wolkenten et al., 2007) it seems unlikely that he was unable to perceive inequity in his environment. Behavioural differences may have been too small or variable to detect in our analyses. This chapter also showed some (albeit limited) evidence that inequity preferences are dependent on the social context (with monkey vs. with bucket). It is possible that if this monkey were paired with a different conspecific, he would respond differently.

The social control task we performed with one of the monkeys suggested that the behavioural effect of inequity was dependent on the social context of the task. However, the behavioural results do not suggest a clear relationship between inequity and value for primates as it has been known to influence value in humans (E. Fehr & Schmidt, 1999; Loewenstein et al., 1989). Possibly reciprocity is also an important factor. Our parametric design in which only one monkey was the actor allowed us to remove effort as a source of variation. However, one can wonder whether we removed an important part of the social context which may have been needed to establish social preferences. Nevertheless, even with only a passive conspecific the effect of inequity on behaviour was dependent on the social context, as could be seen by the lack of an effect in the ‘bucket’ control task.

The necessity of social context does not necessarily mean that the behaviour can only be explained by motives of social preferences. Motives of social preferences are for example, caring about another’s reward or having preferences for equal rewards. Slower reaction times in disadvantageous inequity could alternatively be the result of fear of reprisal by a dominant monkey. Or a faster response time in disadvantageous inequity could be the result of a desire to get to the next trial quicker. Other experiments would be needed to comment on the underlying motives of the monkeys.

Social dominance and inequity related behaviours

Macaques live in social dominance hierarchies (Maestriperi, 2007). There could be an effect of social dominance on the tolerance or sensitivity to inequity. Our experiments cannot answer questions on social dominance as we only tested two animals. We can however add that Monkey A was socially dominant over monkey B. Perhaps dominant monkeys in these particular circumstances are less sensitive to inequity which would account for the lack of a behavioural response in Monkey A.

Unidirectional inequity coding

Most of the neurons we recorded that showed modulations by inequity only showed modulation for one type of inequity. These neurons, therefore, do not encode a combination of own and other’s reward. If this were the case both advantageous and disadvantageous inequity would have modulated the activity of these neurons. Other studies also support the idea that the two forms of inequity are encoded separately in the brain (see chapter 1 for more details). For example, a previous study found that activations in human striatum reflect one form of inequity depending on the wealth of the individual (Tricomi et al., 2010). Also, disadvantageous inequity and advantageous inequity show different patterns of activation in fMRI (Fliessbach et al., 2012). In addition,

advantageous and disadvantageous inequity develop at different ages in both humans (Blake & McAuliffe, 2011; LoBue et al., 2011) and monkeys (S. F. Brosnan, Hopper, et al., 2012).

Alternative explanations

Alternative explanations for inequity encoding neurons could be the magnitude of available reward, or the difference in the rewards. Both of these options have been shown to be correlated with ventral striatum activity in fMRI (Fliessbach et al., 2007; Hsu et al., 2008). However, neither of these models of thinking about other's rewards showed a better fit with our data when looking at modulation of activity on a single neuron level. More importantly, most of the neurons only recorded one type of inequity and not the other. This means that this distinction between advantageous and disadvantageous inequity is important when looking at single neuron activity. It also excludes reward difference and the total available reward from being good models to explain the results of this neuronal data as confirmed by our model comparisons.

The amount of effort to obtain rewards can affect reward inequity (van Wolkenten et al., 2007). In the first version of the task in which the actors changed roles every other trial, we were able to analyse whether effort had an effect on the encoding of reward and inequity. (This analysis was performed by Dr Baez-Mendoza and was therefore not presented in this chapter.) Only a very small amount (15%) of neurons that encoded reward or inequity were also modulated by effort. Thus, there was in fact a small effect of effort in this first version of the task. In the second and third parametric version of the design, only the recorded monkey was the actor. The effort can therefore be considered a constant and excluded as an explanatory factor in this part of the data. Our results do not give enough evidence to draw any firm conclusions about the effect of effort on inequity coding in striatal neurons. This would have to be explored in a separate study.

A limiting factor in our study is that we lacked a non-social control in the neurons that we recorded. It can therefore not be excluded that the inequity modulation in striatal neurons could be a comparison of reward with another reward in the environment, irrespective of the social context. Future experiments should strive to include social context in their design to solve this problem.

How inequity fits in with known striatal function and connectivity

Previously striatal neurons in the area where we recorded have been shown to encode information about rewards (Cromwell & Schultz, 2003; Lau & Glimcher, 2007). In addition to this not only the actual reward and value but also the discounted value is encoded by striatal neurons (X. Cai et al., 2011). Moreover, the striatum and the rest of the basal ganglia are well known for their role in

actions. The encoding of value by the striatum has been shown to be specific for certain actions, commonly referred to as action-value coding (K. Samejima et al., 2005). fMRI studies have also associated the striatum with subjective value coding (Kable & Glimcher, 2007). In addition to the previously shown modulation of reward activity by subjective factors like for instance temporal discounting (Kable & Glimcher, 2007), we have now shown that reward and action related activity in the striatum is also modulated by inequity. Interestingly there are only few striatal neurons that encode the conspecific's reward (Báez-Mendoza et al., 2013). This could mean that inequity is not computed in striatum. Instead, it could possibly be calculated elsewhere and then transmitted to striatum for incorporation of this parameter into action value calculations.

Previous studies have shown that coding of conspecific's reward, at least in part, takes place in the anterior cingulate gyrus. Single neuron recordings in this region have shown a correlation to conspecific's reward (S. W. C. Chang et al., 2013). Neurons in orbitofrontal cortex also show a modulation of their value signal by conspecific's reward (Azzi et al., 2012). In conclusion, different regions in the brain may be involved in calculations of inequity in different ways. The modulations of activity we see in striatum may be the product of some or all of these.

It is important to note that different parts of the striatum have been described to get inputs from different cortical areas (Haber & Knutson, 2010). It is thought that these different striatal regions form parts of different cortical-striatal loops connecting the cortex with the basal ganglia in different locations (Alexander, Delong, & Strick, 1986). Our recordings took place in a span of regions that probably included a combination of these loops, however we did not find any significant clustering of any type of inequity encoding neuron in any particular region. This suggests that modulation of neuronal activity by inequity is probably not confined to a particular part of the anterior striatum. It is important to note that, even though we studied inequity in conjunction with own reward, we found no evidence that inequity encoding neurons belonged to a distinct separate neuronal population of reward neurons. Both anatomical and model selection analyses did not point to these neurons as separate populations. This of course does not mean that there may not still be some functional distinction between these two subsets of neurons. Potential studies on connectivity or studies including the use of molecular markers could reveal whether the neurons we recorded belong to different intermingled classes of neurons within the region. However, this was not the focus of our experiment.

Our experiment shows evidence that activity in striatum is modulated by inequity. It is possible that the modulation of inequity in striatum serves to incorporate this value into action values and determine choices and other behaviour in freely behaving animals. More research is needed to characterise the exact role of various brain regions and their connectivity in inequity related behaviours. It is possible that choices between various amounts of inequity could shed some light on the exact nature of macaques' social preferences. We recorded behaviour in such a task in interleaved sessions with the experiment described in this chapter. The next chapter will present the results of a choice task which can answer how inequity affects choice in macaques.

Chapter 4 – Experiment 2: Social choice

In the previous chapter data was presented on the representation of inequity in striatum neuronal activity. However, the behaviour was relatively unclear so far. We have recorded a limited number of behavioural sessions in which choice trials were performed by one of the monkeys with similar stimuli as used in the inequity study. In this chapter, this additional choice data will be presented to characterise behaviour, more specifically with regards to inequity. This data will also be presented to check its consistency with the data of the animal from the previous experiment. Although this data may be insufficient to draw firm conclusions about social choice, this chapter presents an interesting case study of choices in which we can attempt to understand social preferences in macaques.

In humans, parameters for choice and action (e.g. rewards, effort and inequity) are taken into account differentially dependent on the exact nature of the task. When only one available option for own and other's reward is given, a larger weight is placed upon the inequity between these two rewards (Bazerman et al., 1995). However when a choice is given between two options more parameters emerge. In addition to own and other's reward, a comparison between own rewards is now an important factor in choice. In humans choices, it has been shown that the difference in the magnitude of the two own rewards carries more weight in the decision than the inequity between own and other's reward (Bazerman et al., 1995). In the previous chapter, an experiment was described in which animals were presented with single options that contained predictive cues for own and a conspecific's rewards. In this chapter, I will show choice behaviour in three macaques in which rewards for own and other varied and contained varying amounts of inequity.

Aim

We have seen that there is an inconsistent, but present, effect of inequity on behaviour. One of the aims of studying choices in macaques is to see whether there is a visible effect of inequity on response times and performance behaviours in a choice task that can be related to previously recorded response times in the single option task. In addition to these other behaviours, choices themselves will allow us to examine which parameters affect choice. In more detail we can find out whether macaques would choose to give or withhold rewards from another monkey selectively when the rewards for self are kept equal. Potentially, all of this together could lead to a better understanding of inequity attitude in macaques.

Methods

Animals & Ethics

Four adult male macaques (*Macaca Mulatta*) (Obi, L40, Trident and Virtue) performed a choice task. The animals were housed together with other adult males. The fourth macaque (Virtue) did not participate in the task in which there were rewards for the other animal but only played for own rewards while another macaque (Trident) was present doing the same. This is why only three monkeys are taken into account for analyses of inequity and four monkeys are analysed for effects of own rewards. The four animals were paired into three dyads (Obi and L40; L40 and Trident; Virtue and Trident). Obi's social choice sessions took place with a passive animal (L40). However, the other two dyads alternated choices. All the experimental procedures were approved by the United Kingdom Home Office under the Animals Scientific Procedures Act of 1986.

Data collection

This data was obtained from behavioural sessions which interleaved the sessions that were recorded for the inequity project in the previous chapter for one animal. A section of this data was collected by Raymundo Báez-Mendoza as he was involved in these earlier sessions. For the other two animals, choice data was recorded in training sessions. It was necessary to train these animals on making choices before training them on more complicated social games. Inequity was introduced as a parameter in a subset of these trials to attempt to understand social preferences in macaques. In a fourth animal only (non-social) choices between different own rewards were performed.

Setup and Task Design

The setup was the exact same as in the previous chapter. Two macaques were situated across from one another. On a table in between them a touchscreen spanned the distance in between the monkeys which was used for performing the task. The monkeys could not reach each other but could see each other and shared the use of the touchscreen which they took turns to use. Before and in between the trials the animals held separate touch sensitive keys which were meant to record the exact start of their movements and to make sure the animals' hand was in the starting position in the centre of the screen and static before a new trial started. The passive receiving monkey would not be required to do anything except face forward and not display any disruptive behaviour. Rewards consisted of 0.2ml of Blackcurrant squash diluted 1:10 in water (Ribena, GlaxoSmithKline). In one animal (L40) the task was only performed by him with a passive animal across from him (Obi). In later pairing of animals (L40 and Trident and later L40 and Virtue) the animals switched roles after each trial. In this task, animals were presented with two choice options (Figure 4.1). Options with various amounts of own rewards and various amounts of disadvantageous and advantageous

inequity were used. The amount of times different stimuli were used varied between animals. The reason for this is because the data was gathered during training of the animals for a different experiment and various data sessions that were recorded to test for a general preference for social reward. Different animals needed varying amounts of training. Therefore, this resulted in a dataset with varying amounts of data for different animals. No further data selection was done so all the available choice data was used.

Figure 4.1- Choosing higher rewards in binary choice

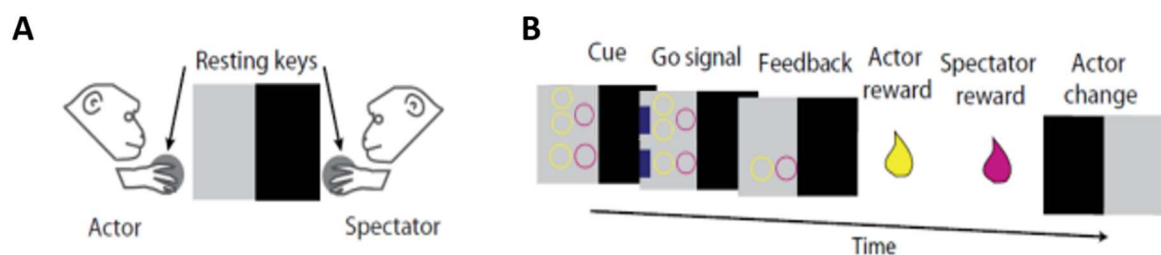


Figure 4.1 Social choice task (A) Animals sat across from each other. A touchscreen rested in between them on a table. Animals were trained to rest their hand on touch keys. (B) Task sequence: Stimuli contained circles and squares to predict the reward outcome. The colour of the circles would indicate who the reward was for. After a short delay the targets would light up, a small square on the edge of the screen, this would be the area of the screen that the animal should touch to perform the task. Then if the animal touched one of the targets within the allowed time window both animals would receive their respective rewards and the roles of actor and spectator would reverse on the next trial.

A range of different options was presented to generate a wider range of different choice conditions (tables 4.1 and 4.2). High rewards were used less than low rewards. High rewards saturate the monkeys more swiftly, resulting in less trials. Another reason is that monkeys work less in sessions with low rewards when these are preceded by high rewards which is disruptive to data collection. Therefore, a smaller range of rewards is preferable and the most used range of rewards for self and other were 0-3 juice drops. When table 4.1 shows the amount each combination of own and other's reward was used in a choice trial. Because two options were always shown to choose from the total is twice the amount of choice trials that were recorded.

Table 4.1- Presented combinations of own and other's reward

		Other's Rewards (Juice Drops)						Total
		0	1	2	3	4	5	
Own reward (Juice Drops)	0	1203(44)	52(21)	484 (21)	321 (13)	25(1)		2085
	1	1679(49)	461(10)	1108(24)	392(16)	47(1)		3687
	2	1341(43)	51(1)	487(14)	566(24)	121(3)	20(1)	2559
	3	1670(50)	217(6)	1004(23)	910 (22)		176(4)	3977
	4	709(24)		68 (1)	607(25)	44(1)		1428
	5	41(1)			202(4)		259 (3)	502
Total		6616	781	3151	2998	237	455	14238

Table 4.1 Numbers indicate totals of choice options that were presented this does not say much about the actual choices but it shows that a wide variation in choice options was used. Numbers in between parentheses show the amount of sessions that these stimuli were used in.

Table 4.2 shows us another display of the presented choices this time as a combination of the difference in own rewards paired with a difference in the other's rewards. This table shows that the large majority of choices only varied in own or other's reward, not both (4819/7119 (68%)).

Table 4.2- Presented options - Own reward comparison vs. Other's reward comparison

		Δ Other's Rewards (Juice Drops)					Total
		0	1	2	3	4	
Δ Own Rewards (Juice Drops)	0	9(1)	26(1)	2255(94)	1271(52)	73(5)	3634
	1	402(26)	137(8)	48(2)	207(9)		794
	2	634(33)		1264(62)	494(21)		2392
	3	149(9)			66(3)	43(2)	258
	4				41(2)		41
	Total	1194	163	3567	2079	116	7119

Table 4.2 Numbers indicate totals of choices presented as a combination of difference in own and other's reward. In total this results in 1194 choices where only own reward is different, 3634 choices in which other's reward is different and 2291 choices in which a combination of own and other's rewards are given. Numbers in between parentheses show the amount of sessions that these stimuli were used in.

Behavioural Analyses

For quantification of performance, I classed errors as trials in which a monkey either did not perform the trial in the allotted time epoch or where the monkey let go of the touch key too early. Any error that occurred before the onset of the stimulus presentation was excluded from analysis. To be clear, performance does not relate to choosing the larger or 'correct' option, it only relates to more general task performance. For response times and choice analyses, only correct trials were used.

Effects of own reward and inequity on performance were analysed using binary logistic regression. From logistic regressions, odds ratios are obtained that give an intuitive measure of how much the grouping based on independent variables increases the odds of observing the dependent variable. The equation for analysis of performance is:

$$P(\text{Correct}) = \frac{1}{1+e^{-(\text{LinC})}} \quad \text{Equation 4.1}$$

with:

$$\text{LinC} = \beta_0 + \beta_1 * W_{\text{Chose}} + \beta_2 * \Delta W + \beta_3 * DI_{\text{Chosen}} + \beta_4 * AI_{\text{Chos}} + \varepsilon \quad \text{Equation 4.2}$$

$$\Delta W = |W_A - W_B| \quad \text{Equation 4.3}$$

$$DI_{\text{Chosen}} = (\max(Z - W, 0))_{\text{Chosen}} \quad \text{Equation 4.4}$$

$$AI_{\text{Chosen}} = (\max(W - Z, 0))_{\text{Chos}} \quad \text{Equation 4.5}$$

In which W is own reward and Z is other's reward. DI and AI stand for disadvantageous inequity and advantageous inequity, respectively. A and B subscripts refer to choice options A and B. Response times were quantified as the time from the onset of the target stimuli to the touch on the screen. Response times were analysed with a linear regression similar to the analysis in the previous chapter. Because there were two options present I chose the regression coefficients which I believed would be equivalent to the regression coefficients used in the single option reward giving task. These resulted in the following regression equation.

$$RT = \beta_0 + \beta_1 * W_{\text{Chose}} + \beta_2 * \Delta W + \beta_3 * DI_{\text{Chosen}} + \beta_4 * AI_{\text{Chosen}} + \varepsilon \quad \text{Equation 4.6}$$

W_{chosen} is the chosen own reward magnitude. Equations 4.3-4.5 were used to calculate the other variables. Choices were also analysed with a binary logistic regression (equation 4.7) similar to the equation used for performance analysis (equation 4.1). The main difference is that the identity of the choice options now mattered so the calculations were done as follows:

$$P(\text{ChoseA}) = \frac{1}{1+e^{-(\text{LinearC})}} \quad \text{Equation 4.7}$$

with:

$$\text{LinearC} = \beta_0 + \beta_1 * \Delta W + \beta_2 * \Delta DI + \beta_4 * \Delta AI + \varepsilon \quad \text{Equation 4.8}$$

$$\Delta W = W_A - W_B \quad \text{Equation 4.9}$$

$$\Delta DI = (\max(Z - W, 0))_A - (\max(Z - W, 0))_B \quad \text{Equation 4.10}$$

$$\Delta AI = (\max(W - Z, 0))_A - (\max(W - Z, 0))_B \quad \text{Equation 4.11}$$

All these statistical analyses were performed with SPSS (IBM). Proportions and proportion CI's were calculated by hand and occasionally checked with Office Excel (Microsoft).

Results

Effects of own reward and inequity on choices.

In total 7119 choices were recorded in four animals (Obi: 5821; L40: 854; Trident: 428; Virtue: 301).

The large majority of this data was recorded in Obi. In all four animals larger rewards were chosen more frequently than by chance (Obi: 85.0(CI±9.1); L40: 91.9(CI±0.074); Trident: 82.8(CI±0.18); Virtue: 87.2(CI±0.045)). In addition to this, logistic regression results indicated that there was a significant relationship between the relative difference in the reward and the frequency with which the larger reward was chosen (Table 4.3). This is visualised in figure 4.2 with the least squares regression line per animal showing that the relationship between choices for larger reward and differences in own rewards is similar for all four animals.

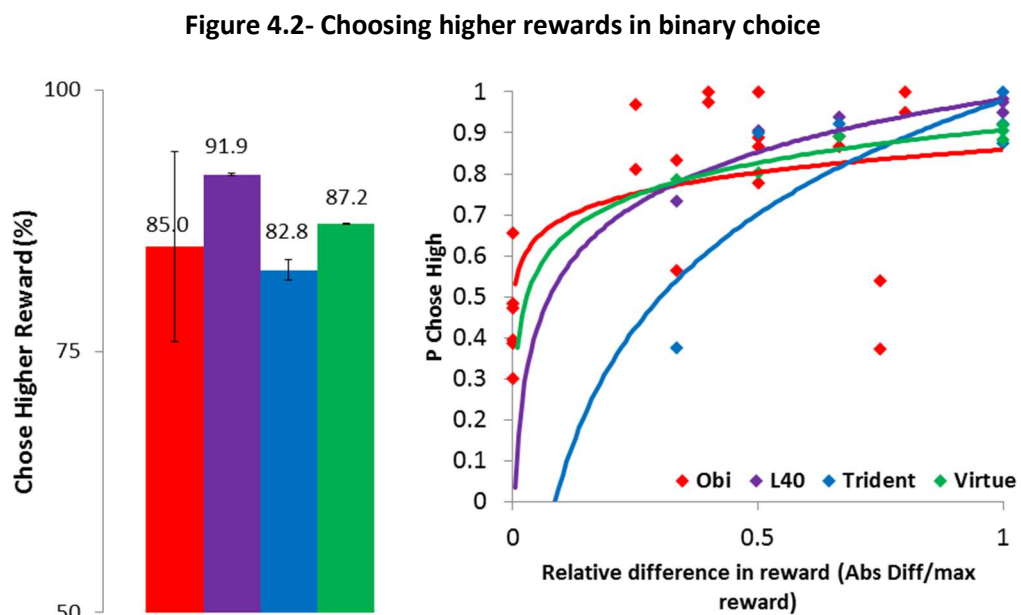


Figure 4.2 Macaques choose higher rewards more frequently. (Left) When given a binary choice the animals choose the higher rewards for themselves more frequently. Some animals have a higher success rate than others but overall the probability of choosing the higher reward ranges between 82.8 and 91.2. Error bars are 95% confidence intervals. (Right) Results separated according to the relative difference in rewards between choice options ((High-Low)/High) All animals choose higher reward more frequently when there is a smaller difference in rewards. In some conditions there is no difference in own rewards. This results in the data points at zero relative difference in reward. Differences in own rewards were standardized for plotting purposes. Other statistics were done using unstandardized variables. Lines are LS fitted logarithmic functions.

Choices were analysed with a logistic regression using own reward and different forms of inequity as independent variables (equation 4.7 – 4.11). Odds ratios obtained from this analysis indicate that when own reward is bigger the odds of choosing this option increase significantly in all monkeys (Obi: (odds ratio:)1.65 (CI: 1.49-1.82), L40: 3.82(CI: 2.77-5.25), Trident: 2.66(CI: 2.02-3.50), and Virtue: 2.73(CI: 1.50-4.98)). Only Obi shows significant changes in choices with inequity. This is possibly due to the larger amount of data in this dataset. A larger advantageous inequity in a choice option increases the odds of choosing that option (Odds ratio: 1.51(CI: 1.39-1.64). Whereas a larger disadvantageous inequity significantly decreases the odds of choosing that option (Odds ratio: 0.88(CI: 0.81-0.96)).

Table 4.3- Logistic regression of choices over own reward and Inequity

Animal	Coefficient	B	S.E.	Wald	P	Odds Ratio	95% CI
Obi	Δ Own Rewards	0.498	0.051	94.6	8.9×10^{-178}	1.65	1.49-1.82
	Δ Adv. Inequity	0.412	0.043	90.8	1.6×10^{-21}	1.51	1.39-1.64
	Δ Dis. Inequity	-0.125	0.044	7.86	0.005	0.88	0.81-0.96
L40	Δ Own Rewards	1.339	0.163	67.4	2.2×10^{-16}	3.82	2.77-5.25
	Δ Adv. Inequity			1.14	.285		
	Δ Dis. Inequity			0.55	.461		
Trident	Δ Own Rewards	0.978	0.140	49.2	2.3×10^{-12}	2.66	2.02-3.50
	Δ Adv. Inequity			0.02	.883		
	Δ Dis. Inequity			0.62	.430		
Virtue	Δ Own Rewards	1.006	0.306	10.8	0.001	2.73	1.50-4.98

Table 4.3 Results from logistic regression. Obtained from Binary logistic regression of choice (Chose A). Regressors: Own Reward A - Own Reward B, Advantageous inequity A - Advantageous inequity B, Disadvantageous inequity A - Disadvantageous inequity B. Odds ratios indicate that when own reward in A is bigger the odds of choosing A increase by 1.65(CI: 1.49-1.82), 3.82(CI: 2.77-5.25), 2.66(CI: 2.02-3.50), and 2.73(CI: 1.50-4.98) respectively per unit of increase in this difference. Only Obi shows significant changes in choices with inequity. Increase in advantageous inequity increases the odds of choosing that option (Odds ratio: 1.51(CI:1.39-1.64). Whereas an increase in disadvantageous inequity decreases the odds of choosing that option (Odds ratio: 0.88(CI:0.81-0.96)). As explained in the methods, because Virtue only performed choices for own reward, no statistics are available for inequity for this monkey.

Effects of own reward and inequity on performance and response times

Performance data was analysed using a binary logistic regression of performance (P (Correct)). The regression coefficients in the model contained 'Chosen Own reward', 'Absolute difference in own rewards', 'Chosen Advantageous inequity' and 'Chosen Disadvantageous inequity' (equation 4.1).

Odds ratios indicate that when the chosen own reward is bigger the odds of performing the trial correctly increase. (Table 4.4) The analysis showed a significant relationship between advantageous inequity and task performance. This was not the case for disadvantageous inequity.

Figure 4.3- Performance in choice trials depends on size of reward

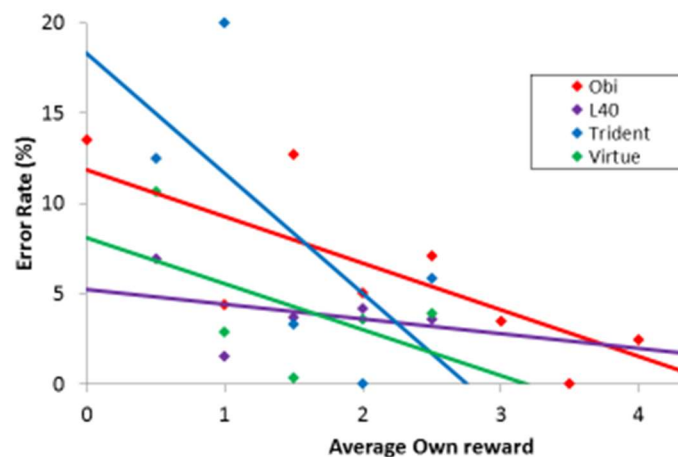


Figure 4.3 The error rate (not correctly performed choices) is higher for choices between lower rewards. Lines are least mean squares lines to show strength and direction of relationship between error rate and reward for each animal.

Response times were also analysed to study whether there were any effects of social reward differences on this parameter. The exact regression coefficients are set out in equations 4.2 to 4.6. Again own reward has a significant effect on response times in each animal. In data recorded from Trident the effect of own reward is a combination of chosen own reward and the difference between own rewards. All animals showed a significant effect of inequity on response times. However which form of inequity was represented in this data was different per animal. (Table 4.4 and Figure 4.4) When all the significant coefficients for performance and response times are taken together, these results suggest that larger advantageous inequity resulted in faster response times and a higher performance rate. This does not hold true for each form of inequity, but each animal did have significant results in at least one form of inequity in both behavioural measures.

Table 4.4- Regression of performance and response times over own reward and Inequity

Logistic Regression on correct vs. error trials						
Animal	Coefficient	B	S.E.	Wald	P	Odds Ratio
Obi	Chosen Own Reward	.400	.038	109.7	1.2*10 ⁻²⁵	1.491
	Δ Own Rewards	-.018	.038	0.217	.641	.982
	Chosen Adv. Inequity	.151	.047	10.28	.001	1.163
	Chosen Dis. Inequity	-.001	.045	.0002	.987	.999
L40	Chosen Own Reward	.463	.056	69.50	7.7*10 ⁻¹⁷	1.590
	Δ Own Rewards	.255	.079	10.41	.001	1.290
	Chosen Adv. Inequity	.541	.071	57.90	2.8*10 ⁻¹⁴	1.718
	Chosen Dis. Inequity	.243	.139	3.066	.080	1.275
Trident	Chosen Own Reward	.599	.064	88.54	5.0*10 ⁻²¹	1.821
	Δ Own Rewards	.064	.081	0.632	.427	1.066
	Chosen Adv. Inequity	.209	.074	7.954	.005	1.232
	Chosen Dis. Inequity	.261	.144	3.305	.069	1.298
Virtue	Chosen Own Reward	.659	.081	66.79	3.0*10 ⁻¹⁶	1.933
	Δ Own Rewards	-.013	.117	0.013	.908	.987
Linear Regression on Response times						
Animal	Coefficient	B	S.E.	t	P	95% CI
Obi	Chosen Own Reward	-20.3	3.045	-6.7	2.9*10 ⁻¹¹	-26.266 -14.328
	Δ Own Rewards	2.74	3.263	.84	.401	-3.658 9.134
	Chosen Adv. Inequity	-.042	2.687	-.02	.987	-5.309 5.225
	Chosen Dis. Inequity	-33.3	4.493	-7.4	1.3*10 ⁻¹³	-42.148 -24.532
L40	Chosen Own Reward	-17.6	7.707	-2.3	.023	-32.731 -2.455
	Δ Own Rewards	-7.66	11.64	-.66	.510	-30.518 15.190
	Chosen Adv. Inequity	-35.5	8.796	-4.0	6.1*10 ⁻⁵	-52.811 -18.256
	Chosen Dis. Inequity	-2.79	22.98	-.12	.903	-47.936 42.350
Trident	Chosen Own Reward	27.6	10.86	2.6	.011	6.310 48.982
	Δ Own Rewards	-34.3	15.01	-2.3	.023	-63.777 -4.776
	Chosen Adv. Inequity	-38.8	12.61	-3.1	.002	-63.551 -13.996
	Chosen Dis. Inequity	29.6	29.09	1.0	.309	-27.569 86.800

Table 4.4 Results from regressions of additional behavioural measures. (Top) Logistic regression on performance data. Regressors: Chosen Own reward, Absolute difference in own rewards, chosen advantageous inequity, chosen disadvantageous inequity. The calculated odds ratios indicate that when the chosen own reward is bigger the odds of performing the trial correctly increase. All animals that were tested for the effects of inequity showed an effect of either advantageous or disadvantageous inequity but this was different in all animals and was also different for different behavioural measures. (Bottom) Values obtained from linear regression of same regressors on the response times of all the animals. Because this is a somewhat noisy measure not enough data was collected in Virtue to use this data in this regression. Again own reward has a significant effect in each animal. In Trident the effect of own reward is a combination of chosen own reward and the difference between own rewards. All animals showed a significant effect of some form of inequity of the chose option on response times. However which form of inequity was represented in this data was different per animal. When taken together all these results suggest that higher inequity resulted in faster response times and a higher performance rate suggesting that animals may in fact be inequity seeking.

Figure 4.4- Plotted response time means over four variables in linear regression

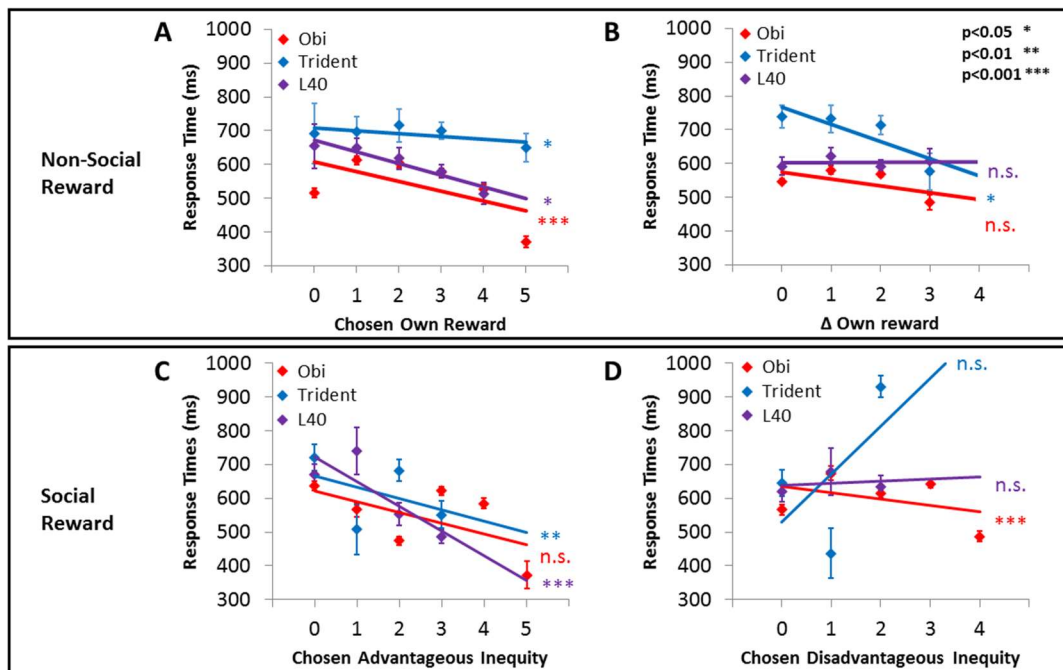


Figure 4.4 Linear regression of non-social and social reward variables on choice response times Lines are least mean squares lines to show strength and direction of relationship between response times and reward parameters. Four different reward variables are used as regressors. Chosen own reward (A) and the differences in own rewards (B) are two non-social variables of which only Chosen own reward seems to affect response times significantly in all animals. Large differences are also observed in two out of three animals when looking at advantageous inequality (C). Disadvantageous inequality shows far less consistent results with only one animal showing a significantly decreased reaction time with higher levels of inequality (D).

Social choice

To study the effects of social rewards on choices in more detail the trials with equal own rewards were examined separately. Regrettably this partition of data excluded all but one animal from analysis of choices as all other animals did not contain enough trials in which own reward was kept constant. Because own rewards largely dominate the choices between options, it is in conditions where own rewards are constant that we hoped to see the direction and strength of social preferences. In the data from the one animal that was left, it was possible to have a closer look at the general effect of the other's reward magnitude on choices without the interference of own reward effects. Conditions with ten or fewer trials have been excluded from this analysis. Choice proportions were quantified for two different grouping categories (Figure 4.5). First they were calculated for differences in other's reward. Next, the data was also separated according to the type of choice regarding inequality. Choice proportions show that, in general, Obi chooses higher rewards for the other less frequently. This was true for all three types of choices. However, this effect does

not seem linear and it should be noted that when the difference in rewards is 2, Obi significantly more often chose a larger reward for the other. The effect is significantly stronger in choices where the animal has an equal option available. Possibly choices with two different forms of inequity are harder which creates more errors in their preferred behaviour.

Data from other animals is plotted to check general consistency. As a general rule, Obi chooses lower rewards for the other more frequently as the difference between other's rewards becomes larger. Obi chooses larger rewards for the other monkey less frequently in all comparisons between own and other's reward. However, this effect is more prominent in conditions where the animal is choosing between equal and unequal conditions. 'More vs Same' ($0.3461(CI\pm0.030)$) and 'Same vs Less' ($0.3887(CI\pm0.039)$) both show significantly more anti-social choices compared to 'More vs Less' choices ($0.4687(CI\pm0.031)$).

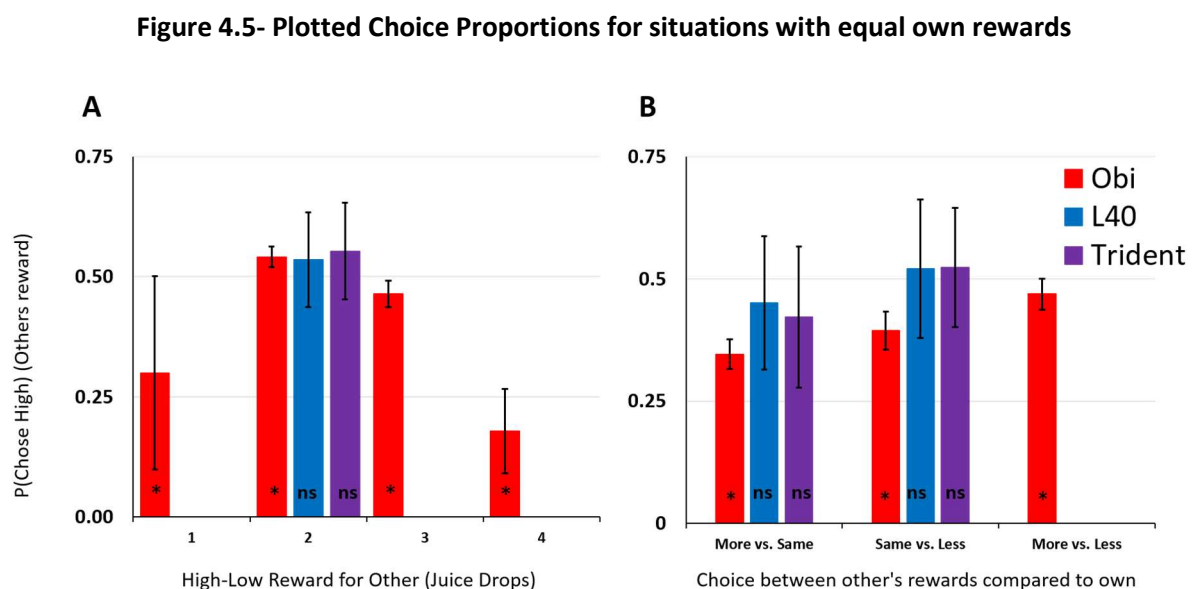


Figure 4.5 Choice proportions with 95% confidence intervals I only collected enough data from one animal (Obi) in which choices were presented where own reward was kept equal. Conditions with 10 or less trials have been excluded from this analysis. Data from other animals is plotted to check for gross inconsistencies. **A** Obi chooses higher rewards for the other less frequently as the difference between other's rewards becomes larger. (1, N=20; 2, Obi, N=2062; 2, L40, N=99; 2, Trident, N=94; 3, N=1261; 4, N=73) **B** Obi chooses higher rewards for the other less frequently in all comparisons between own and other's reward. However this effect is more prominent in conditions where the animal is choosing between an equal and an inequitous condition. More vs Same ($0.3461(CI\pm0.030)$) and Same vs Less ($0.3887(CI\pm0.039)$) both show significantly less choices for higher rewards for the other a compared to More vs Less choices ($0.4687(CI\pm0.031)$).

Conclusions and Discussion

In choice trials, larger own reward causes a higher choice proportion for these options, a quicker response time and a higher performance rate. In addition, the absolute difference in own reward has an effect on response times and performance, but not in all animals. Since these effects are not present in all animals, the effects are possibly more subtle and possibly convoluted with or overshadowed by the effects of the chosen reward. In conjunction with effects of own reward, there are some varying results suggesting that both advantageous and disadvantageous have an effect on behaviour in choice trials. Interestingly, there is a consistent decrease in response time with increasing advantageous inequity, also Obi's choices were affected by both advantageous and disadvantageous inequity. These results show that macaques are sensitive to other's rewards and inequity in choices. However their attitude towards inequity depends on their own reward as well as the difference between the offered rewards for the other. It would take another study with a specifically designed payoff matrix to decipher the exact nature of macaques' inequity attitude. Although we attempted to study social preferences in post hoc analyses in this choice data presented in this chapter, the mixture of many different conditions containing varying own rewards, others rewards and inequity levels was not optimal to study social preferences and this should be taken into account if another attempt at this is to be made.

The effects of inequity on choice behaviour were very variable. Advantageous inequity of the chosen options seems to have a stable effect on performance whereas both advantageous and disadvantageous inequity seem to affect response times differently for different animals. It is important to note that the amount of data in three of these four animals was very limited. The only animal that had a substantial amount of data recorded in this task was Obi. This shows in the most consistent results obtained from these data. It is still interesting that the others still show variable but significant effects of inequity in their response times and performance rates. One would expect, with these results, that if we were to record more data in this task we would see a significant effect of other's reward on choice in the other animals as well, in particular when recording more trials with equal own reward.

It is interesting that when only looking at trials with equal own rewards, Obi shows a preference for anti-social choices (choice options in with the least amount for the other. This is a very consistent result that appears to become stronger with a larger difference between these other's rewards. This larger effect for a larger difference in other's rewards mimics the effect on preferences for larger own rewards. Both show a stronger effect if the difference between these becomes larger. The difference between these two, is that the animal prefers less reward for the other and more for

himself. From these choice proportions one could conclude, that Obi behaves advantageous inequity seeking and disadvantageous inequity averse. Advantageous inequity seeking is consistent with the results obtained for performance and response times for advantageous inequity which showed an increase in performance and a decreased response time. Another factor to consider was that Obi's social choice sessions took place with a passive animal. Possibly, reciprocity is important to this task and that if the task is performed by only one animal, this animal will not want the other to receive rewards and will minimise this.

These results are an indication that macaques have social preferences but that these are subtle and variable. More data was needed for the other subjects in conditions where own rewards were kept equal. General choice proportions of L40 and Trident in these social choice conditions were consistent with the choice proportions of Obi. Possibly if more data were gathered for these animals, this would result in a more solid conclusion about whether these animals also prefer if other animals have less reward.

Data gathered during choice task training resulted in an interesting case study of social choice behaviour. Own rewards and both forms of reward inequity affected choices, response times and performance in this social choice task. In one case, it was clear that this animal preferred for the other to get less reward regardless of inequity. Whether this is also true for the other animals, or macaques in general, remains to be seen.

Chapter 5 – Experiment 3: How monkeys solve the coordination problem

When presented with multiple options, one is not always clearly superior over another. Imagine two people on a narrow path walking towards each other. They can either both swerve to the right or to the left to continue their journey. However, because it is not obvious which way they should move they face a ‘coordination problem’. There are different ways in which they can solve this challenge. One example is to follow ‘rules’ (everybody always moves to left) or always stopping to wait what the other does. In any case, to proceed safely they will need to watch their conspecific and base their decision on what the other does. In this chapter this situation is simulated in a game. Two monkeys are given two options to choose from. Both options pay four drops of juice when both animals choose it. However, the game only gives one drop for each, when the animals do not coordinate their choices. As discussed before, the Nash equilibrium is often used to predict the outcomes of games such as these. In this case, this is not possible because the game has two equally stable Nash equilibria. Because the options do not contain a payoff dominant option (an option that pays more than the other), it can’t be predicted from the payoff matrix which option will be chosen. Macaques have been known to coordinate in the wild and in experimental settings (see chapter 1 for details) but it is not known how these animals will behave when faced with two options of exact equal value. In this experiment I studied how macaques deal with the coordination problem and whether there is any evidence for a particular strategy in their behaviour. Analyses of the choices show that monkeys coordinate on a significant amount of trials and do this by choosing the same option in trains of choices but also by behaving in a win-stay lose-shift manner. Whether monkeys use these strategies as conscious choices for a strategy or whether they are a product of reinforcement learning remains to be explored.

Aim

Monkeys have shown many signs of social behaviour and interactions. More specifically, many primates have been shown capable of playing coordination games in an experimental setting. Many of these experiments consisted of two monkeys having to pull levers simultaneously to get access to rewards but some also used two-by-two games such as a stag hunt. What these experiments do not tell us is how macaques respond when faced with options of equal value. In this chapter, I present an experiment in which monkeys needed to coordinate their choices to receive larger rewards in the presence of two possible coordination options of equal value. The aim of this experiment is to characterise macaque behaviour in these matching games. If the macaques converge to an option, it

will be important to learn how they do this. In studies of coordination on human subjects, the Win-Stay Lose-Shift strategy has been described as an important strategy to model behaviour. Thus, another aim of this experiment is to study whether the animal's choices seem to be according to this well described strategy. To study strategy, it is important to distinguish it from much simpler strategies that are just a product of monkey behaviour in binary choice tasks, without the presence of another monkey. Therefore an analysis of strategy will include picking the same option multiple times in a row to distinguish this from a more elaborate win-stay lose-shift model. More importantly, I will address whether the employed strategies result in an increase in coordination.

Methods

Animals & Ethics

Three male macaques (*Macaca mulatta*) were housed together with other male macaques and used in two dyads to perform tasks together. The monkeys' names were L40, Trident and Virtue. Two of them were cage mates (Trident and Virtue). In these tasks the pairs of monkeys (dyads) were required to make choices which would contribute to each other's outcomes. To prevent any problems in the home cage as a result of testing, only non-cagemate dyads have been tested so far (L40 playing with Trident and L40 playing with Virtue). The animals were trained on the use of the touch key, juice spout and touchscreen for several months before training them to perform the task, they also all underwent training in a separate task in which they alternated choice trials (see chapter 4) to help them get used to another animal sitting across from them and to wait for the other animal if needed. All the experimental procedures we did were approved by the United Kingdom Home Office under the Animals Scientific Procedures Act of 1986.

Set up and Task Design

Three monkeys were trained to play a 'combined choice' task. In this task, two monkeys were required to make binary choices within a four second time window. The design of this study was based on a study by Sarah Brosnan (S. F. Brosnan, Wilson, et al., 2012). If both animals made a choice, their payoffs would systematically depend on the choices of both monkeys. The choice options were presented as normalised grey fractals of equal sizes on a touchscreen. These fractals were changed every 50-300 trials. The fractals were changed when both animals chose the same option on all trials for ± 20 -50 trials. In other words, convergence to one option was not allowed to continue for too long as I aimed to prevent overtraining animals on choosing the same option without exploring the other options. The characteristics of each game are determined by the nature of its payoff matrix. In the next chapter, for instance, the same task was used but the nature of the experiment changes because of important differences in the payoff schemes that were used

(Chapter 7). In the game presented here (figure 5.1, B), both objects have equal value and yield an equal payoff for each animal but only if they both choose it. It is therefore not important which object the animals choose, only that they choose the same object. The challenge in this game is that both options have equal value and it may not be easy for the animals to decide which option to choose.

Figure 5.1 – Combined choice task with matching game payoff scheme

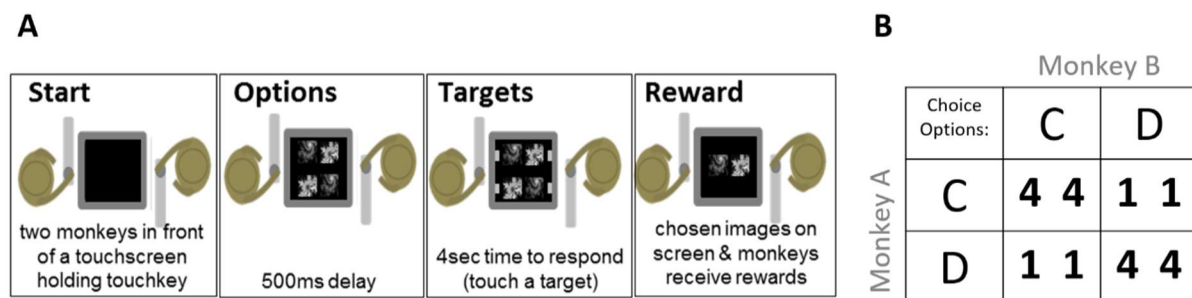


Figure 5.1 ‘Combined choice task’ with ‘matching game’ payoff scheme (A) Top view of the setup. Monkeys hold a touch key on opposite sides of a touchscreen. Then the choice options come on. After 500ms the targets come on. Targets indicate that the animals are allowed to move and choose. They get 4 seconds to both indicate their choice by touching one of the targets. After the four seconds have passed, the chosen stimuli stay on the screen for 500ms and the monkeys receive their rewards one after the other with 500ms in between. The order in which they receive rewards switches on every trial to counterbalance any temporal effects on value of the rewards. (B) The table indicates the payoffs for animals in 0.15ml juice drops given the chosen options of both animals.

Behavioural Analyses

In total 7206 combined choice trials were recorded from two different dyads (table 6.1).

Table 5.1 – Numbers of trials collected in animal dyads and fractal sets

Dyad	Image Sets	Trials	Sessions
L40 & Trident	28	4687	31
L40 & Virtue	7	2519	14
Total	35	7206	55

Table 5.1 Numbers of trials collected in various conditions. The data was collected as training in preparations for other games. Sessions were of varying lengths. Less data was collected in the second dyad as one of the animals had been previously trained on this task (L40) which made training a lot quicker for the second dyad.

Choices and response times were recorded while the animals performed the described task.

Response times were defined as the time between the targets’ onset and the time of touching a

target of choice. Only the first choice counted, thus, animals were not permitted to change their minds. Occasionally the animals would try to touch another option after they already indicated their choice. However, this didn't happen in most trials and this data was not recorded. If one of the monkeys let go of his touch key before the targets were presented or did not touch one of the targets within the four seconds this would result in an error. Error trials were not used in the data analyses. Choices were first analysed by using a logistic regression to see whether animals significantly managed to coordinate more effectively over time.

$$P(\text{Coordination}) = \frac{1}{1 + e^{-(\beta_0 + \beta_1 * \text{Fractal set trial number} + \epsilon)}} \quad \text{Equation 5.1}$$

In this equation the 'fractal set trial number' is the chronological numbering of trials within fractal sets. In addition, I also studied the way the animals converge to one option over time. This option is also referred to as the 'focal point'. The trial on which an animal reaches the focal point is defined as the first trial in which he has chosen that option in 10 trials in a row. The first 9 trials are not taken into account. Thus, if the trial of reaching the focal point is 1, that means that the animal chose that object exclusively for the first 10 trials. Response times were analysed to find out whether these were different in coordination vs. non-coordination. In addition to this to account for effects of the previous trial this was also added as a variable. A linear regression was performed on data for separate animals in dyads. To look at separate animals in separate dyads independent tests of means (t-test) were done to obtain individual differences between subgroups. Two other factors were also included in this model. To check whether the increased speed of responses might be an effect of more coordination trials taking place later in the trial block, 'Fractal set trial number' was also included in the model. Additionally, to account for the possible effect of the other's response time I also included this as a factor on the response times. This resulted in the following model:

$$\text{Response Time} = \beta_0 + \beta_1 * \text{Coordination} + \beta_2 * \text{Coord. Previous Trial} + \beta_3 * \text{Fractal set trial number} + \beta_4 * \text{RT Conspecific} + \epsilon \quad \text{Equation 5.2}$$

To obtain differences in separate animals between specific conditions independent tests of means (t-test) were done. In all these tests, groups were tested for unequal variance with F-tests. T-tests for unequal variance were used where appropriate.

Animals often chose the same option for multiple trials in a row (persistence). According to the definition of a Win-stay Lose-shift (WSLS) strategy, these stretches of choices would be classed as

WSLS. I wanted to differentiate whether a win-stay lose-shift strategy was used separate from persistence of choices. I therefore classed trials in two ways based on strategies for each animal. The first strategy was whether an animal chose the same option as on the previous trial ('Stay' in equation 5.4). The second strategy, 'win-stay lose-shift' ('WSLS' in equation 5.4), was whether an animal coordinated on the previous trial (and therefore received the larger reward) and stayed with the same choice on the current trial 'or' did not coordinate on the previous trial and chose the other option on the current trial. Whether the amount of trials played for each animal was different from chance level was determined with binomial tests. However to actually study the effectiveness of these strategies (whether they increased coordination) the strategies were used as variables in a logistic regression on the occurrence of coordination (equation 5.3).

$$P(\text{Coordination}) = \frac{1}{1+e^{-(\text{LinC})}} \quad \text{Equation 5.3}$$

where LinC is defined as,

$$\text{LinC} = \beta_0 + \beta_1 * \text{StayA} + \beta_2 * \text{StayB} + \beta_3 * \text{WSLSA} + \beta_4 * \text{WSLSB} + \varepsilon \quad \text{Equation 5.4}$$

In this way I could assess how much the behaviour of animals according to strategies resulted in higher levels of coordination. This was done for animals separately in each dyad.

Results

Animals coordinated more effectively over time due to perseverance

When performing the coordination task monkeys took varying amounts of trials to converge to one of the two options. The option on which they eventually converged is referred to as the 'focal point' of coordination. Choosing the same option trial after trial irrespective of the outcome, can be referred to as 'perseverance'. In many cases it took some time for both of the animals to reach this focal point (Figure 5.2 A). The amount of trials that the animals performed in a set of fractals increases the likelihood of them choosing the focal point. Coordination likelihood also increased significantly with the trial number in both animal dyads. (L40&Trident: $\text{Exp(B)}=2.53$, $\text{Chi-square(df=1)}=31.03$, $p=2.5*10^{-8}$; L40&Virtue: $\text{Exp(B)}=2.3$, $\text{Chi-square(df=1)}=6.98$, $p=0.008$) Thus, more experience with a given set of objects increased the chance of coordination. In example data (figure 5.2) we can see that monkeys coordinate on the two different options at the beginning of a session. However, the monkeys later go on to coordinate on only one of these options with more experience with a fractal set making non-coordination less frequent.

Figure 5.2 – Example data from single sessions matching games

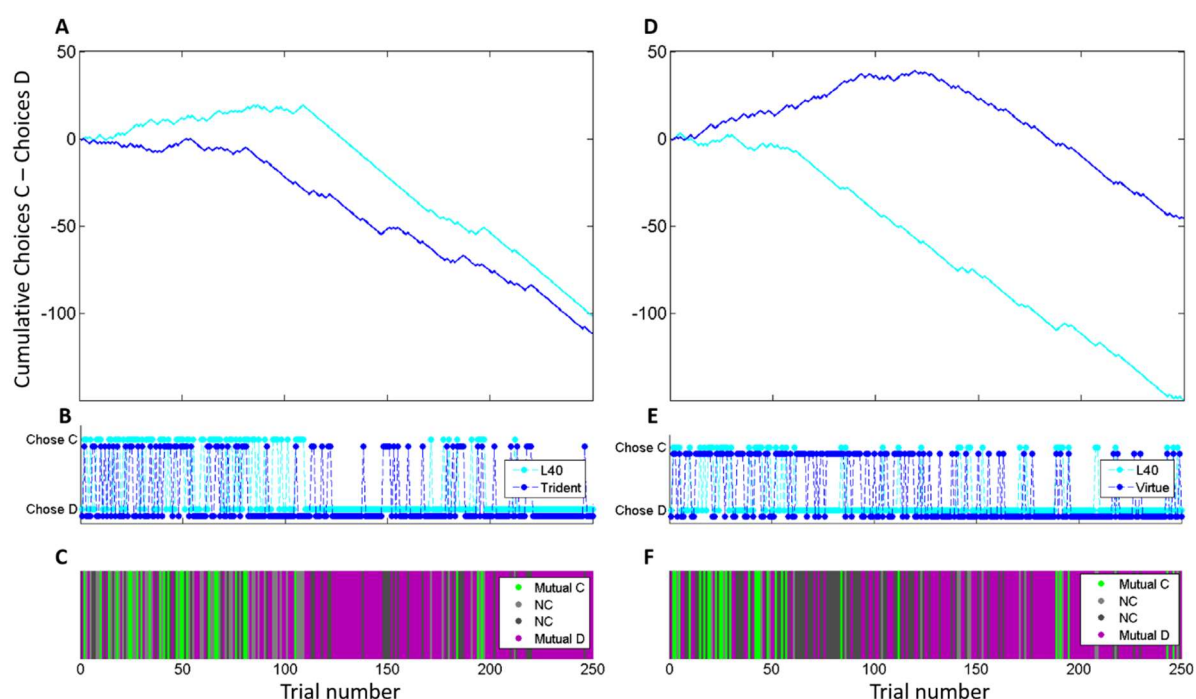


Figure 5.2 Example data from single sessions illustrate representative behaviour in two dyads. (A&D) Plots display the first 250 trials of a session with L40 and Trident (A) and a session with L40 and Virtue (D). The lines indicate the number of choices for option C minus the number of choices for D. When the slope is positive the animal chose C and if the slope is negative the animal chose D. Choices are also displayed in B and E with corresponding colours. (C&F) Plots of combined choices show in green and purple trials in which the animals coordinated. Non-coordination is displayed in light and darker grey. In the two example sessions a lot of coordination is visible throughout the session, but as the session progresses this coordination mainly takes place on one particular option.

The number of trials in which individual animals in a dyad reached the focal option is correlated in one dyad (figure 5.3) (Pearson Correlation: L40&Trident: $r=0.72$, $p=0.00006$). It should be noted that the other dyad was excluded from this type of analysis because it only had 7 data points. Data points and the (least squares regression) line through these points showed a similar pattern. This correlation indicates a convergence on the focal point. L40 is often the first of the monkeys to reach the focal point. This could possibly indicate that he is usually the one to instigate this strategy of perseverance.

Figure 5.3 – Monkey pairs converge on focal option at different but related point in time

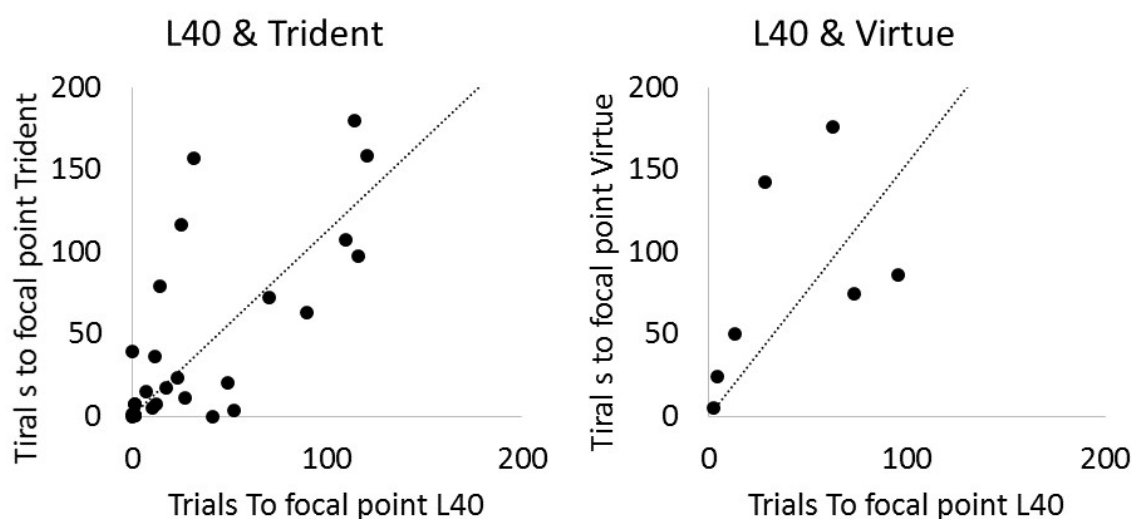


Figure 5.3 Monkey pairs converge on focal option at different but related points in the sessions. Scatterplots contain points indicating the trial on which each of the monkeys converged on the focal option. L40 is often the first monkey to choose this option 10 times in a row. The trial in which the monkeys reached the focal point are correlated, displaying a convergence of the monkeys on the focal option. L40 had a tendency to be quicker to reach the focal option than the other animals in the pairs. This caused a shift in the data-points to the upper left quadrant of the plot.

Role of early preferences on convergence

Per given set of objects the animals varied in their initial responses (choices in the first 10 trials). In some fractal sets the animals already started off by choosing the fractal they would eventually choose most often in a high proportion. In other fractal sets, this was not the case and an animal chose their focal option less than half of the time. Of interest is whether these early preferences correlate with how quickly the animal reaches a point where he chooses that option all the time. This is the case in two out of three animals (Pearson Correlation: L40: $R=-0.63$, $p=0.001$; Trident: $R=-.55$, $p=0.005$). The third animal (Virtue) does not have enough data points ($N=7$) to perform this test. However the least squares regression line follows the same general trend as the effects in the other two animals.

Figure 5.4 – Early preferences correlate with converging on focal option

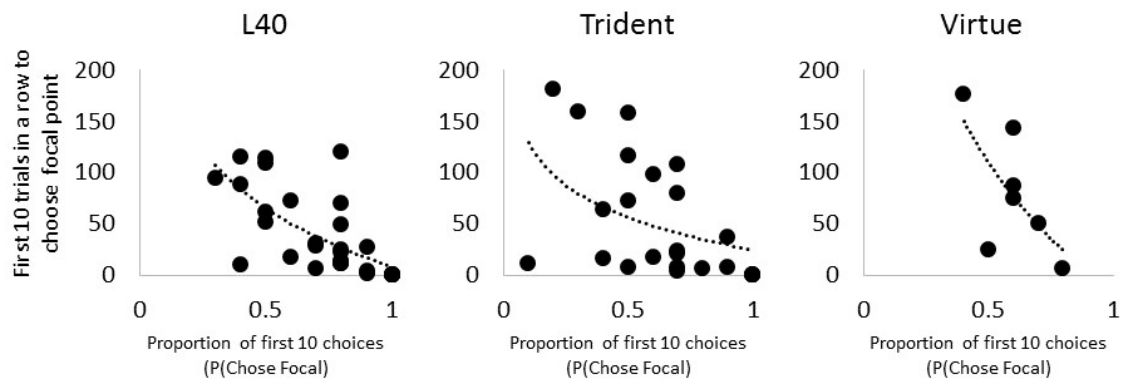


Figure 5.4 Early preferences can help us predict how quick animals reach focal point. Although there is some variation. The choices in the first ten trials are significantly correlated with the speed at which the animals reach their focal point.

Figure 5.4 shows that L40 often has a higher proportion of choosing the focal option. This could possibly indicate that his preferences are a more important factor in the choice between options as focal points. This is consistent with the result that he is often the first monkey to reach the focal option.

Response times indicate awareness of other's choice

In summary so far, monkeys seem to coordinate more over time in a given set of options. They also converge upon a focal option. When studying this in more detail, their early preferences indicate which option they will converge upon and how fast they will reach this point. From the monkeys' choices it is clear that they value coordination, however what is not clear is whether they are aware while performing the trial that this will be a coordination trial and will be more rewarding. To further investigate this, response times were analysed with a regression model including coordination on current trial and coordination on previous trial as factors. The other's response time and the trial number are also taken into account as control variables (equation 5.2).

Figure 5.5 – Response times are lowest when coordinating after coordination

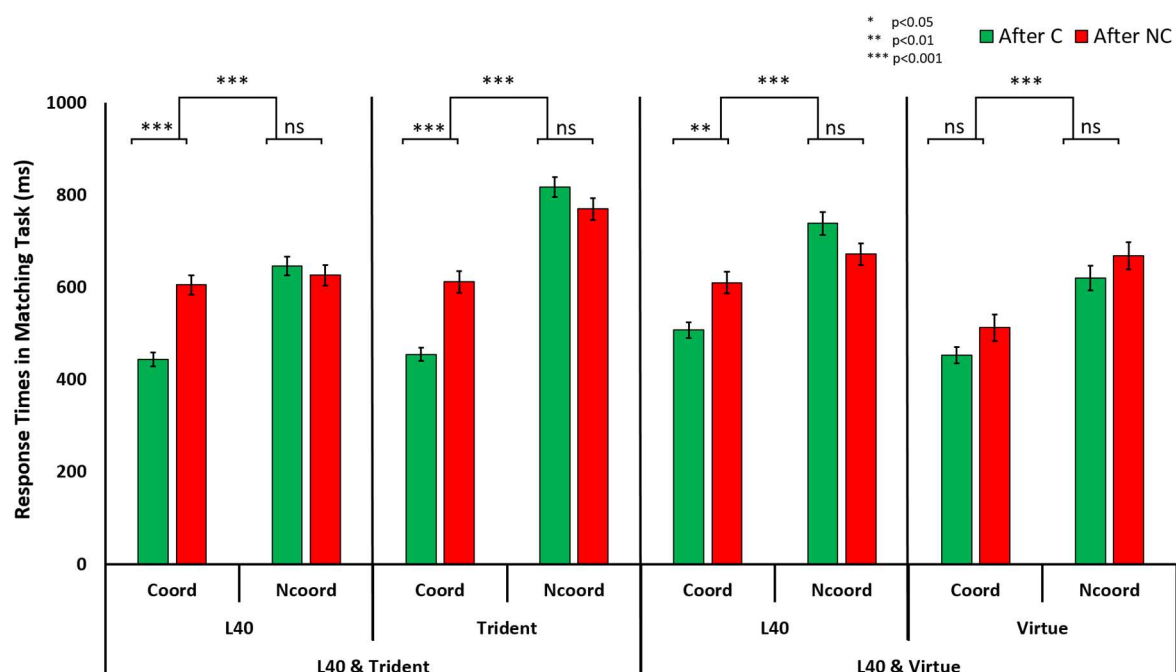


Figure 5.5 Response times are lowest when coordinating after another coordination trial. Bars indicate mean response times of the specified conditions. Statistics represent outcomes of independent t-tests. In all animals coordination is significantly faster than non-coordination, however after a trial in which the animals coordinated the response times are even faster in two out of the three animals. No significant differences in response times are observed in non-coordination trials. Error bars are standard error of the means.

Coordination choices were performed significantly faster in all animals (L40: $B=-83.1(CI\pm68.7)$, (t-test :) $p=0.018$; Trident: $B=-481.0(CI\pm66.1)$, (t-test :) $p=2.98*10^{-45}$; Virtue: $B=-268.5(CI\pm75.3)$, (t-test :) $p=3.67*10^{-12}$). Moreover, there was an effect of coordination in the previous trial on the response times in two animals (L40: $B=-92.4(CI\pm44.3)$, (t-test:) $p=4.5*10^{-5}$; Trident: $B=-100.3(CI\pm43.5)$, (t-test:) $p=6.4*10^{-6}$). This effect was not significant in the response times of the third animal (Virtue: $B=-43.6(CI\pm52.2)$, (t-test :) $p=0.10$). However, Virtue's response times did show a trend consistent with the effect which was observed in the other animals.

Both perseverance and Win-Stay Lose-Shift choices facilitate coordination

The monkeys have a tendency to choose the same trial as on the previous trial (L40: 76.5% (Binomial test :) $p<0.001$; Trident: 69.2%, $p<0.001$; Virtue: 70.5%, $p<0.001$). This very simple perseverance of choices possibly explains why early preferences seem to be such a good predictor for how quickly the animals will converge on a focal option. However this strategy can't be successful if the same choice of image is also maintained when it doesn't pay as much as before. A strategy that has been

well described (see chapter 1) is the Win-Stay Lose-Shift strategy. In the win-stay lose-shift strategy, when a player gets a large or better than expected reward he stays at that strategy, when it gives him a worse than expected reward he shifts to a different strategy.

The monkeys behave according to the win-stay- lose-shift strategy more than chance level (L40: 70.2% (Binomial test :) $p < 0.001$; Trident: 70.1%, $p < 0.001$; Virtue: 70.1%, $p < 0.001$). Because win-stay lose-shift overlaps with perseverance both strategies are taken into account in one model (equation 5.4 and 5.5) to check the added value of the win-stay lose-shift behaviour in the attempt to coordinate. The analysis showed that there was a significant effect of perseverance (stay) on coordination. This possibly accounts for the long periods of trials in which the animals just coordinate and don't change their choices at the end of sessions. However, in addition to this, choices according to the win-stay lose-shift strategy also significantly increase the odds of coordination. Importantly, the WSLS strategy gives a larger increase in coordination when the Trident and Virtue play according to this strategy. Possibly, this is because L40 is often the first to start choosing the focal option more often and shows 6-7% more perseverance than the other monkeys. Notably, this does not result in more coordination due to this strategy as can be seen from the similar odds of coordination for the 'stay' strategy in L40. Importantly, all results are consistent between the two dyads as is shown by comparison of the overlapping confidence intervals between these outcomes.

Conclusions and discussion

Monkeys manage to coordinate their actions to gain higher rewards in a task in which there is no clearly dominated option. In addition to this the animals seem to be aware of the choice of the other as shows from their response times. Furthermore, coordination on the previous trial even further decreases the response times. Possibly this shows an advantage to habitual behaviour.

Monkeys establish coordination by means of preferences and strategy

The aim of this experiment was to establish how monkeys would coordinate given that options were of equal value. Monkeys often choose the same option many times in a row regardless of the outcome. This is called perseverance. When both animals do this for the same option it leads to a convergence on a focal option resulting in highly successful coordination. Although there is no particular reason to choose one option over another animals sometimes choose one option more than another in the first ten trials already. These seemingly 'early preferences' are correlated with the speed with which the animals reach their focal point and are possibly an advantageous strategy

in themselves. Sometimes coordination is more important than the exact outcome and people who can make choices with very little information can cause quicker convergence and as a result more coordination. In this case L40, although he instigates the convergence, ends up contributing less to the overall coordination. This is supported by the results that show that L40 is faster to respond in trials and also faster to reach perseverance on a focal point. However his trials classed according to strategies in general result in a smaller contribution to improving coordination. In conjunction, the win-stay lose-shift strategy in Trident and Virtue is vastly more successful at improving coordination. This is not to say that this instigation by L40 is not important. What is remarkable, is how L40 persevered persistently until the other animal finally followed. An example of this was shown in figure 5.2 D where L40 chose a particular option almost all of the time persistently for about 75 trials while Virtue was still choosing the other option slightly more on average. After that time, Virtue finally gave in and started choosing L40's image of choice too.

Strategies only work when not everybody uses the same one

In addition to perseverance, animals also behave according to a win-stay lose-shift strategy, again resulting in higher proportions of coordination resulting in larger rewards for the animals. Win-stay lose-shift behaviour is more intuitive and rational than perseverance. It is a strategy that is directly linked to the outcome of the previous trial. However there is a paradoxical nature to this strategy when applied to the matching game. Imagine a situation where the monkeys choose opposing options on one trial and receive only a small reward. The animals should 'according to the strategy' both change their choice. If so, this will again result in non-coordination and so forth. The same is true for perseverance. If both animals persevere on different options this will result in constant non-coordination. The important point to realise here is that coordination itself has to be reached by learning that choosing the same option as the other is more profitable and to then try and optimise these types of combined choices. Strategies alone are not enough. Strategies only serve their purpose if only one animal uses them at a time. Let us revisit the analogy used earlier in this chapter of two people approaching each other on a narrow path. If one individual always moves to one side this makes it easier for the other person to choose which way to move in repeated encounters. Note that this explanation only works if only one person perseveres first and the other follows. Alternatively, in the case of win-stay lose shift this is slightly different. If the two individuals walk into each other by accident the next encounter will only be more successful if only one of the animals changes strategy. What is similar in both strategies is that the strategies only serve their purpose, the improvement of repeated coordination, when only one player uses them at a time. Possibly this explains why the win-stay lose-shift strategy results in a more successful increase in coordination for

Virtue and Trident. L40 showed more perseverance in his choices, allowing Trident and Virtue to establish coordination in a trial and error, win-stay lose-shift manner.

Rewards are most likely the driving force to establish coordination

Even though there is sufficient evidence to suggest that animals behave according to strategies, there is no reason to believe that animals are aware that they are doing this or that they are consciously choosing a strategy. The important thing to note is that primates both human and non-human most likely make most of their choices for one reason, to gain rewards. In the task that was used here coordination is directly linked to these rewards so coordination cannot be separated from rewards for analysis. The rewarding nature of coordination in this task is supported by the analysis of response times which showed that animals respond quicker when they coordinate and even more so when they coordinated on the previous trial and, thus, coordination is more likely on the current trial. It is therefore important to note that there is no assumption that the animals coordinate because of an inherent reward to coordination.

What next?

In this chapter, we have learned that animals can coordinate even when the available options have no clear 'better option'. We have also considered how they achieve this. So where do we go from here? The next question is whether the monkeys would coordinate on a larger option even if there was some temptation not to. This can be answered by studying cooperative games. In the next chapter, I will describe an experiment in which monkeys will be faced with games in which there will be increasing rewards for non-coordination to answer whether these same monkeys will forego immediate rewards to establish a stable level of cooperation. In this experiment, again, I will not only focus on the question whether the monkeys cooperate. I will also try to illuminate 'how' they achieve cooperation and what the contributing factors are. What I have learned about how the monkeys coordinate is instrumental to this goal. As cooperation is in fact a type of coordination, one can wonder whether monkeys partially use the same strategies to establish cooperation as well. Alternatively one can also wonder whether the monkeys use other strategies that are more complex and not applicable to the game in the current chapter like for instance Tit for Tat (see chapter 5). In any case the knowledge of how monkeys coordinate will allow us to distinguish what is unique about cooperation and whether the ability to coordinate translates into the ability to cooperate as well.

Chapter 6 – Experiment 4: From coordination to cooperation

Coordination and cooperation are necessary for the survival of social species. While coordination only requires the organisation of actions to work together, cooperation also requires overcoming an initial risk or a cost to cooperate. For some time now, monkeys have been known to coordinate and cooperate. Yet, not much is known about how monkeys make decisions in coordination and cooperative situations and how their behaviour is influenced by other players. It is also still unclear whether the monkeys are able to solve these tasks by simply using non-social information (like previous choices and rewards) or whether their choices also depended on the choices of the other monkey. In this experiment, two monkeys (*Macacca mulatta*) played economic games to obtain rewards. The payoff for each monkey was dependant on not just their own but also the others' choice. The specific payoff matrices resulted in coordination and cooperation games. These games provided the monkeys with the option of working together to obtain larger rewards over time. The difference between coordination and cooperation games consisted in the amount of reward given for 'not cooperating' when the other monkey cooperated. When reward for not cooperating increased, both monkeys coordinated and cooperated less. Importantly, this decline did not eliminate the cooperative behaviour. Despite the immediate cost or risk, the monkeys still cooperated in a significant number of trials. Moreover, the monkeys' behaviour, which can be viewed as according to popular strategies like 'Tit-for-tat' and 'Win-stay Lose-shift' increase cooperation. In contrast, if the animals no longer have access to the other's choices, strategies are no longer useful or even detrimental to the levels of cooperation. Together these results lead to the conclusion that monkeys can work together in economic games. When given access to the other's choices they use this information to cooperate and gain larger rewards over time.

Aim

The aim of this experiment was to characterise various aspects of cooperative games played by monkeys. At the start of the study there were a handful of studies showing that Macaques could play coordination games. As these games only vary from cooperative games in one parameter we thought it would be interesting to investigate whether monkeys would be able to perform cooperation and how the games would influence behaviour. Amongst others the following questions will be answered: Do macaques cooperate? If so, do they use other's choices to do so? Do they use strategies? To what end do they behave according to strategies? Does strategizing increase cooperation or just facilitate its initiation? Do the animals play differently when they cannot see the choices of the other animal and play the game like a normal choice game with another monkey in

the room? Do monkeys learn to cooperate over time? I will attempt to answer all of these questions in this chapter.

Methods

Animals & Ethics

Two adult male macaques (*Macaca Mulatta*) were trained to perform a combined choice task. These animals were not housed together but group housed in separate rooms with other male monkeys. Animals were previously trained to come into primate chairs and sit in setup for extended periods of time. Animals went through extensive key touch and touchscreen training before embarking on a training scheme involving simple touch, choice and then a matching task protocol (chapter 5). All the procedures described in this chapter were approved by the United Kingdom Home Office under the Animals Scientific Procedures Act of 1986.

Set up and Task Design

The setup was identical to that described in chapter 5. Two monkeys were situated across from one another in the setup. Embedded in a table in front there was a touchscreen. The monkeys could not reach each other but could see each other and shared the use of the touchscreen. In between trials the animals held metal touch keys which were also embedded in the table. A trial would only start if both monkeys were holding their touch keys. Rewards consisted of 0.15ml drops of Blackcurrant squash diluted 1:10 in water (Ribena, GlaxoSmithKline) delivered through metal spouts with 150ms in between juice drops. Trial timing and juice delivery were controlled with Matlab (Mathworks).

The task was identical to the 'combined choice task' described in chapter 5. In this task two monkeys make choices after which the payoff is dependent on the combination of these choices. When a trial starts a grey background comes on. After 500ms the stimuli appear. On both ends of the screen 2 greyscale fractals appear that are normalised to have the same luminosity as the background. Their positions are pseudorandomised and counterbalanced over 24 trials.

Figure 6.1 – Combined choice task design

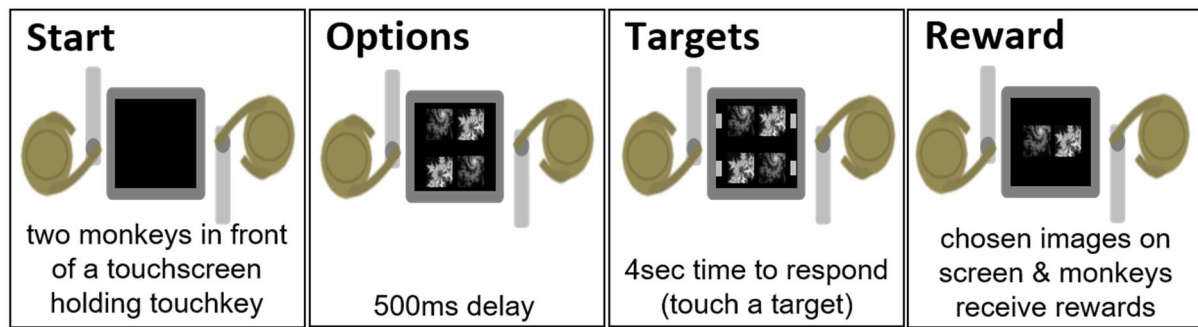


Figure 6.1 Combined choice task design At start of trial a grey background comes on (black in diagram), after 500ms normalised greyscale fractals appear, after another 500ms targets appear, animals now have 4 seconds to both respond, if animals have both chosen the stimuli they chose stay on the screen and rewards are delivered after 500 and 1000ms. The animals alternate in receiving their juice first or second.

After another 500ms the targets are presented. These are small grey rectangles grey colour that appear on the side of the screen next to the choice objects. The target onset is the signal for the monkeys to indicate their choices. They can now let go of the touch key and touch the target of their choosing.

By varying the payoff schemes the animals were made to play six different games (figure 6.2). These games contained two coordination options of which one (CC=4 drops each) payed more than the other (DD=2 drops each). In the most simple coordination game the animals would both receive 1 drop for non-coordination, similar to the game discussed in chapter 5. These games varied in one payoff only. This was the amount of reward received for choosing D when the other animals chose C. Because this reward ‘tempts’ the monkeys away from coordinating on the highest option it will be referred to as the ‘Temptation’ reward or value in the rest of this chapter. This is also the common term for this value in popular descriptions of the prisoner’s dilemma.

Figure 6.2 – Diagram of payoff schemes from coordination to cooperation

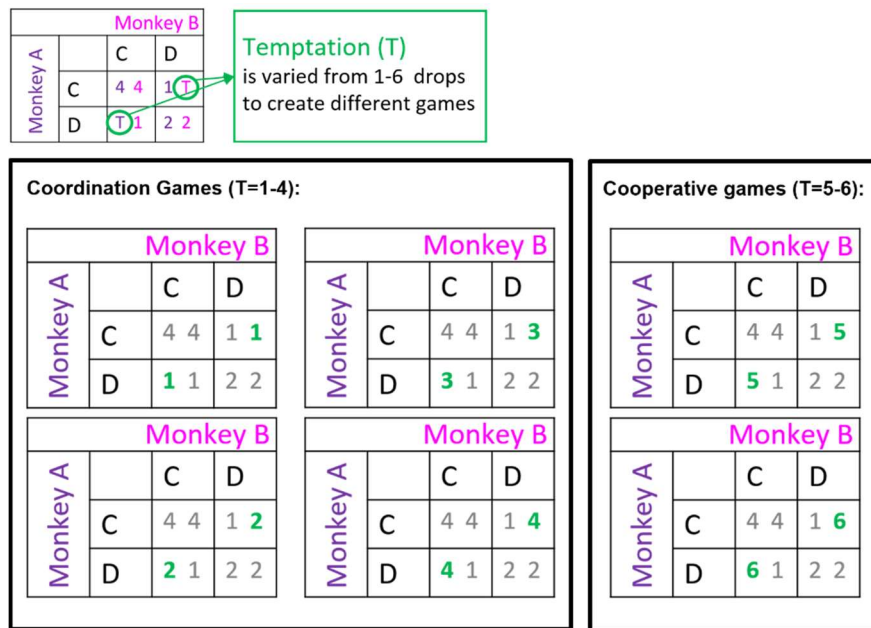


Figure 6.2 Diagram of the payoff schemes performed in the combined choice task. The real task design in the combined choice is in the payoff schemes. The payoff determines what the optimal strategy is and how interdependent the monkeys' choices are. In this experiment six different payoff schemes were used with various amounts of temptation for choosing D. In 4 coordination games the temptation does not exceed the amount to be gained from

When looking at the games more closely it is easy to recognise the characteristics of the prisoner's dilemma as the temptation in these games exceeds the amount monkeys receive for mutually cooperating. In coordination games, choosing CC can also be referred to as choosing the 'pareto efficient' option (the option at which no monkey can get a larger reward without making another worse off, see chapter 1).

Wall control

To investigate whether monkeys use the information from the other's choices, a ± 12 cm high wall was placed in the middle of the screen. This obstructed the monkeys' views of the others' choices. They were still able to see each other, perceive the other's rewards and general arm movements. They could not see the other half of the screen and the other monkey's hand while he was touching the screen. 2948 correct trials were recorded in this condition spread over three games (see table 6.1).

Behavioural Data Collection

Choices and responses were recorded on each trial along with payoffs, reward timing, and errors. In total 16573 correct trials were recorded in one dyad (Table 6.1). This experiment will eventually also be repeated in more dyads however that data collection is still ongoing.

Table 6.1 – Numbers of trials collected in various conditions

	Image Sets	Trials	Sessions
Temptation 1	20	3184	22
Temptation 2	12	1256	12
Temptation 3	11	1271	12
Temptation 4	11	1750	13
Temptation 5	18	4772	26
Temptation 6	9	3578	16
Total	81	16573	101
Temptation 1	5	843	7
Temptation 5	6	1417	9
Temptation 6	3	688	6
Total	14	2948	22

Table 6.1 Numbers of trials collected in various conditions Sessions were of varying lengths and blocks with different games were recorded in a total of 123 sessions with a total of 95 sets of images in a total of 19521 trials

Behavioural Analyses

Response times were studied using correlations and linear regressions. Analyses of cooperation, choices and strategies were done by means of binary logistic regressions. Statistics were calculated with SPSS (IBM) and Excel (Microsoft). To test whether the choice of the other monkey within trials had an effect on choices of the animals, logistic regressions were performed on the data. Data was split into games to compare between the games. These logistic regressions tested whether choices by one animal were more likely based on the already known choices of the other. To be clear, for this analysis, only trials in which the animal of interest chose second were used.

$$P(\text{ChoicesOwn}) = \frac{1}{1 + e^{-(\beta_0 + \beta_1 * \text{ChoicesOther} + \varepsilon)}} \quad \text{Equation 6.1}$$

It is important to note that using variance inflation factors, I determined that reward and coordination could not be viewed as separate (uncorrelated) coefficients in games with lower temptation values (T=1: VIF Payoff=4.8; T=2: VIF Payoff=7.2; T=3: VIF Payoff=2.6). However with higher temptation values the payoff is not as correlated with coordination anymore and can

therefore be seen as a separate measure (T=4: VIF Payoff=1.7; T=5: VIF Payoff=1.4; T=6: VIF Payoff=1.8). To analyse response times I used the same model of coordination and trial history as I used in the previous chapter for the games. However, in this experiment to separate reward from coordination only the T=4-6 games were included in this analysis. The model this time included an addition term for reward (equation 6.2).

$$\begin{aligned} \text{Response Time} = & \beta_0 + \beta_1 * \text{Coordination} + \beta_2 * \text{Coord. Previous Trial} \\ & + \beta_3 * \text{Reward} + \beta_4 * \text{Fractal set trial number} + \beta_5 * \text{RT Conspecific} + \varepsilon \end{aligned} \quad \text{Equation 6.2}$$

To perform strategy analyses trials were classed according to three strategies for separate animals according to the following rules. These three strategies were perseverance (stay), Win-stay Lose-Shift (WSLS) and Tit-for-Tat (TFT). All strategies depended on combinations of current and previous trial (CT and PT) own and other's choices and payoffs (See chapter 5 for further explanation of strategies).

$$\text{Stay} = (\text{ChoiceCT} = \text{ChoicePreviousTrial}) \quad \text{Equation 6.3}$$

$$\begin{aligned} \text{WSLS} = & (\text{PayoffCT} \geq \text{PayoffPT}) * (\text{ChoiceCT} = \text{ChoicePT}) + \\ & (\text{PayoffCT} < \text{PayoffPT}) * (\text{ChoiceCT} \sim \text{ChoicePT}) \end{aligned} \quad \text{Equation 6.4}$$

$$\text{TFT} = \text{FirstTrial} * (\text{ChoiceCT} = 1) + (\text{ChoiceCT} = \text{ChoiceOtherPT}) \quad \text{Equation 6.5}$$

The effects of strategies on cooperation were analysed by means of logistic regression. As the strategies were too highly correlated to use them in one model their effect on cooperation was assessed separately using different models.

$$P(\text{Cooperation}) = \frac{1}{1 + e^{-(\beta_0 + \beta_1 * \text{Stay} + \varepsilon)}} \quad \text{Equation 6.6}$$

$$P(\text{Cooperation}) = \frac{1}{1 + e^{-(\beta_0 + \beta_1 * \text{WSLS} + \varepsilon)}} \quad \text{Equation 6.7}$$

$$P(\text{Cooperation}) = \frac{1}{1 + e^{-(\beta_0 + \beta_1 * \text{TFT} + \varepsilon)}} \quad \text{Equation 6.8}$$

Results

Do macaques take turns to respond?

A feature of the task is that the animals get a period of several seconds to respond. I was interested to see how the animals would spend this time. As the first chooser both monkeys have similar response times (L40: 406ms (± 12 ms, SEM); Trident: 426ms (± 3.5 ms, SEM)). However as second chooser L40 took more time than Trident to respond (L40: 1257ms (± 13.4 ms, SEM); Trident: 896ms (± 4.0 ms, SEM)) I aimed to test whether there was any evidence that animals ‘waited for each other’ or ‘took turns’. The alternative hypothesis to this was that first or second choices were based on arbitrary divisions in two similar but shifted response time distributions. Thus, the null-hypothesis is that the animals have overlapping distributions of response times and that the random location of a trial in these response distributions determined which animal chose first. Based on this, one would expect to see a general positive relationship between response times purely based on the conditions in the trials which will often be the same for both animals, or alternatively no relationship is the conditions have no effect on response times. A second hypothesis that follows from this, is that a general clustering of first and second choices could result in a negative relationship between response times overall as a disproportionate amount of data will have a fast response from one of the macaques and a slow response from the other.

Table 6.2 – Correlation coefficients for response times suggest animals may take turns

Correlation Coefficients between Responses L40 & Responses Trident			
	Overall	Only L40 First responder	Only Trident First Responder
Temptation 1	-0.12	0.28	0.39
Temptation 2	-0.18	0.21	0.38
Temptation 3	-0.26	0.20	0.25
Temptation 4	-0.21	0.31	0.29
Temptation 5	-0.19	0.20	0.41
Temptation 6	-0.19	0.36	0.21
Overall	-0.18	0.27	0.34

Table 6.2 Correlations of response times. Correlation coefficients (Pearson’s r) show that there is a significant overall negative correlation between response times of the two animals in all games. In addition to this, when examining groups of data based on the first responder there is a positive correlation between response times. These results support a clustering of responses as first and second responder possibly supporting that animals ‘take turns’. All coefficients were significant with $p < 0.001$.

Results from correlation analyses show a negative correlation between response times of the monkeys, this supports the hypothesis that response times cluster as first and second choosers. In

addition to this, there is a positive correlation within the groups based on who chose first. It is likely these positive correlations are the result of the division of the data.

Overall Coordination and Cooperation in the combined choice task

Monkeys behave differently when given different games to play. This can be observed in example data (Figure 6.3). In a coordination game the animals converge on a focal option (option C) very quickly at which time they only make very sparse mistakes by choosing D. In this game defection results in a lower reward for both. In a cooperative game monkeys often coordinate repeatedly. Although, in contrast, there is more switching between options and there are more coordination failures. Ultimately the dyad tends to fail to coordinate on a focal option in these games in the given amount of trials (200-600 trials, varying lengths, average fractal set trial number in T: 5 = ± 265).

Figure 6.3 – Example data, Coordination and Cooperative games

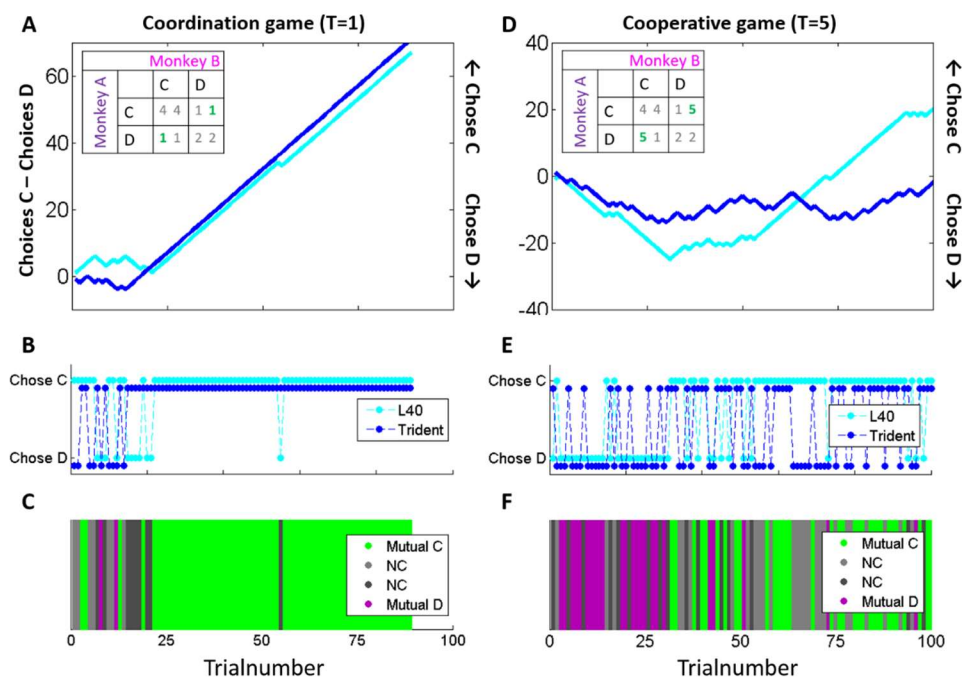


Figure 6.3 Example data in Coordination to Cooperation games Figures in A and D show example sessions with a simple coordination game (Temptation=1) in A and a cooperative game in D. B and E visualise that in the coordination game there is some swapping of choices at the start but most trials after that display constant choosing of the dominant option. E shows that in a cooperative game animals swap between choice options more and start off by choosing mutual defection more at the start followed by more cooperation (Mutual C) later interleaved with trials where one of the animals defects resulting in non-coordination (light and dark grey).

Coordination and cooperation in the different games can be compared by their overall levels of cooperation and coordination. If the null hypothesis is that animals choose randomly and independently one would expect 50% of trials to be mutual choices for C or D. For cooperation or choices for mutual C this is 25%.

Figure 6.4 – Overall Coordination and Cooperation Levels

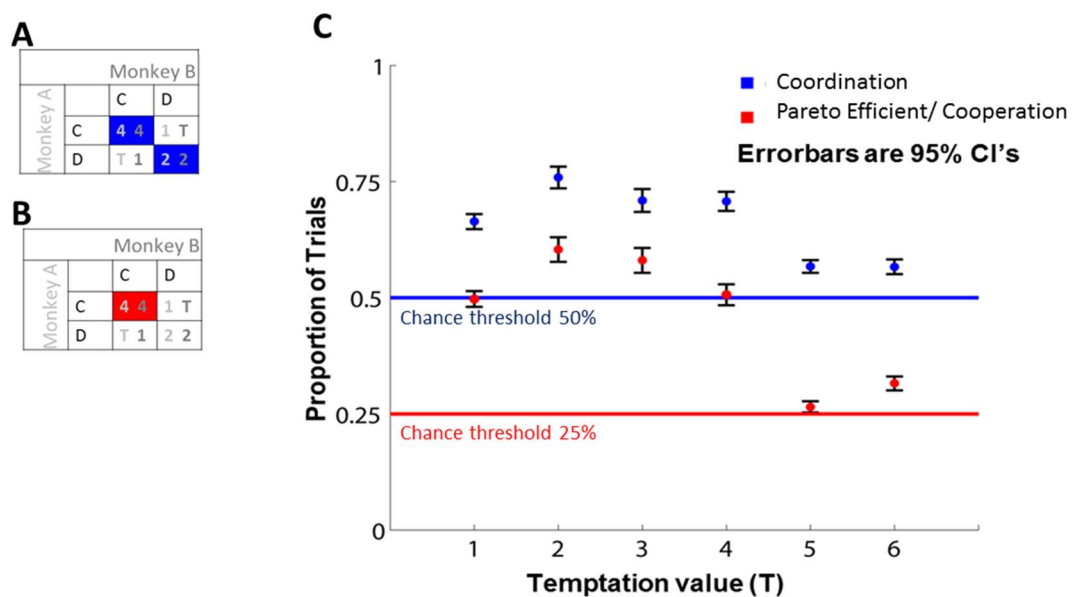


Figure 6.4 Overall Coordination and Cooperation levels. (A) Coordination is indicated in blue and defined as any trial on which the animals choose the same option. (B) Only in cooperative games can choosing the highest coordination option be called ‘cooperation’. However in the other games this option is the Pareto efficient option: The option at which no player can get a higher pay off without making another player worse off. (C) Coloured lines indicate chance levels for different options. All amounts of coordination and cooperation are statistically above chance level. Trial numbers can be found in Table 6.1.

In all games, I observed above chance level coordination and cooperation. Coordination ranges from 55% in the prisoner’s dilemma with 5 juice drops for temptation to 75% in the game with 2 juice drops for temptation. Importantly, cooperation levels were also above chance levels ranging from 27.8% to 62.6%. All of these percentages were above their respective chance levels given the amount of data they were derived from (Binomial tests of all levels resulted in $p < 0.001$). As both monkeys were required to respond within four seconds, the monkeys had an opportunity to see what the other was choosing, when they were the second animal to respond. Both monkeys were more likely to choose C if the other already chose C when they were the second chooser (Logistic regression (equation 7.1); Odds ratios for L40: 2.1, 6.8, 3.8, 4.3, 1.6 and 1.5 for temptation values 1 to 6 respectively; All Wald statistics are significant with $p < 0.01$); Odds ratios for Trident: 3.4, 3.5,

2.6, 3.4, 1.4 and 1.4 again for temptation values 1 to 6; All Wald statistics are significant with $p < 0.01$ except $T=6$ which was significant with $p < 0.05$). The same effect is also visible comparing confidence intervals of conditions displayed in figure 6.5.

Figure 6.5 – Monkeys choose C more frequently if the other already chose C in that trial

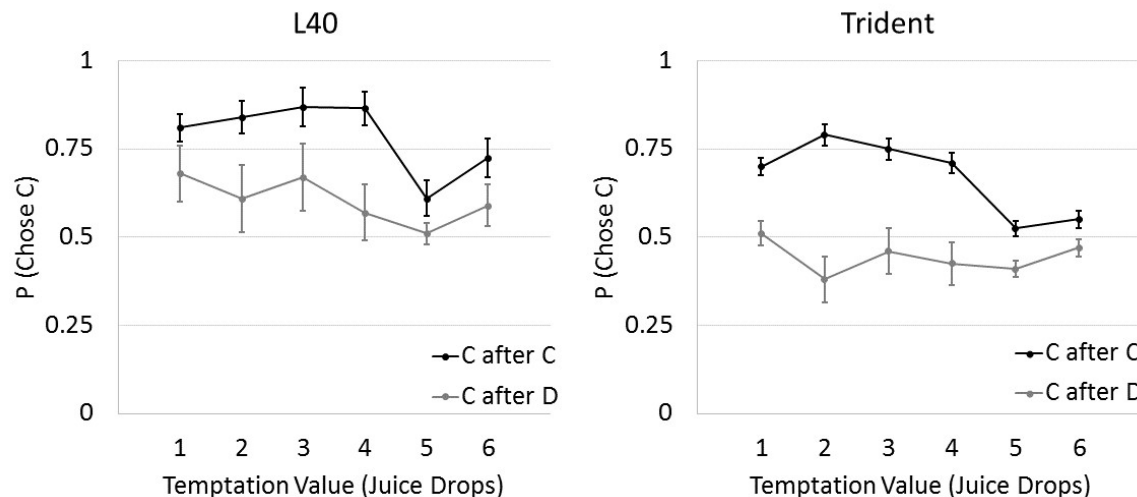


Figure 6.5 Monkeys choose C more frequently if the other already chose C. Do monkeys use their access to the other's choice? When looking at second chooser behaviour only, both monkeys choose C more frequently when the other already chose C. Also the proportion of choosing C after the other chose D doesn't differ significantly between the games.

Response times as a result of coordination and rewards

As also seen in the previous chapter, coordination coincides with large decreases in response times.

These are much larger differences than the differences we see with own rewards in chapters 2, 3 and 4. Possibly the animals have such large variation in response times because of social factors that the smaller effects of reward on response times are now harder to capture. Reward and coordination are collinear in the first coordination game which makes it hard to separate these two. In the previous chapter we saw that coordination had a significant effect on response times, however this was distinguishable from rewards. In higher temptation games the payoff is separable from coordination as the magnitudes of rewards are now divided over coordination and non-coordination. This allows us to analyse, in these games, whether the changes in response times are due to the better payoff or simply coordination of actions. When analysing response times with both coordination and payoff in games with $T=4-6$, response times of L40 decrease significantly with coordination. To test whether this effect is due to coordination or payoff we tested these variables in one equation.

Figure 6.6 – Animals respond faster when they coordinate

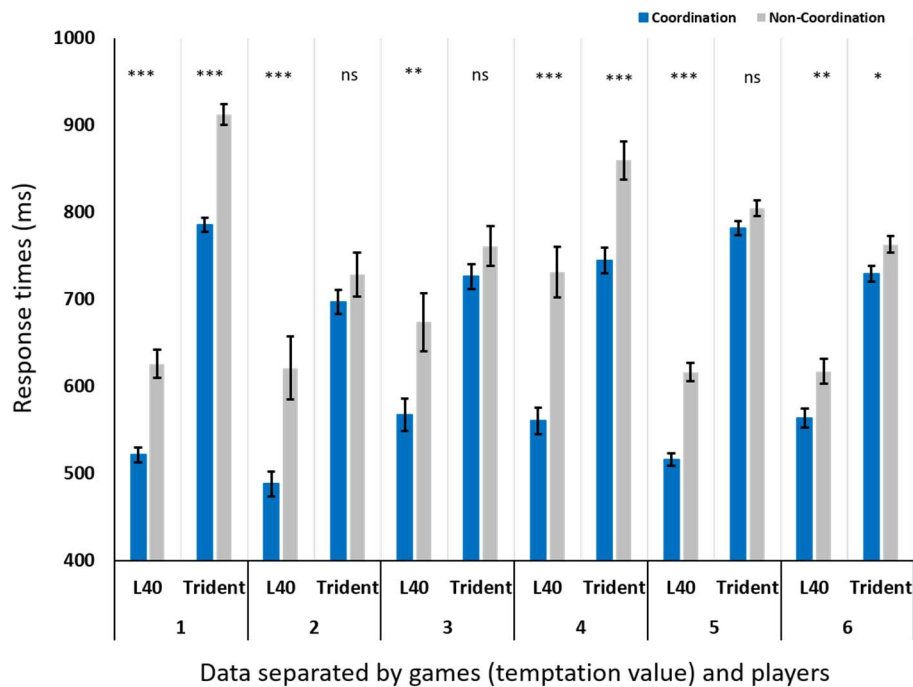


Figure 6.6 Animals respond faster when they coordinate overall but in trident this effect is much smaller in PD's. In all games, both monkeys have shorter response times when they coordinate. This indicates some in-trial knowledge of what the other's choice is as coordination is a result of both monkey's choices. Coordination tends to result in higher rewards than non-coordination which probably accounts for this effect.

There is no significant variance explained by payoff over high temptation games in data from L40. (Linear regression (equation 7.2): Coordination: $B = -26.7$ (t-test :) $p < 0.05$; Payoff: $B = -.99$ (t-test :), ns.; Trialno.: $B = 0.08$ (t-test:) $p < 0.001$; Others Choice.: $B = -.23$ (t-test:) $p < 0.001$;) . Possibly the effects of payoff are smaller compared to the effects of the trial conditions and social effects and are therefore no longer distinguishable from noise. In Trident the effects are the opposite, with significant effects for rewards but not for coordination (Linear regression (equation 7.2): Coordination: $B = -2.9$ (t-test :), ns.; Payoff: $B = -13.5$ (t-test:), $p < 0.001$.; Trialno.: $B = 0.07$ (t-test:) $p < 0.001$; Others Choice.: $B = -.16$ (t-test:) $p < 0.001$;) . The much smaller effect of coordination on response times in high temptation games for Trident can also be seen in figure 6.6.

How do animals cooperate? Choosing in proportions

In the previous analyses we have looked at frequencies of single and combined choice options.

Before moving on to more elaborate strategy analysis it is important to point out that a singular option choosing may not always be the only possible efficient outcome. Given a choice proportion of

Figure 6.7 - Payoff as a result of monkey choice proportions as compared to choice frequencies

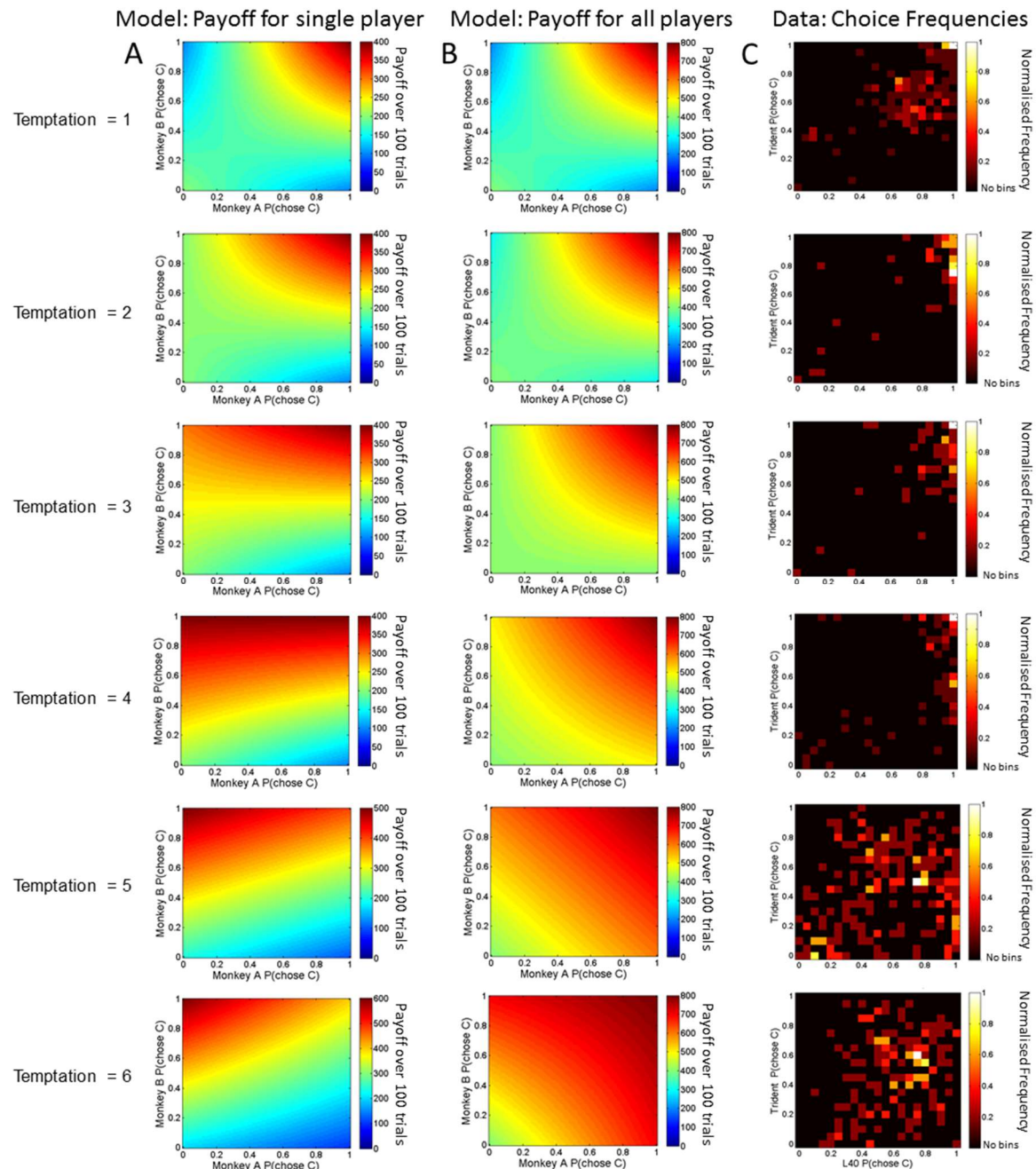


Figure 6.7 Modelling payoff over multiple trials as a result of proportions of choices. Choosing one single option in theory results in the best payoff however choosing options in certain proportions can also improve chances of gaining reward as this increases chances of obtaining the temptation rewards. This illustrates that monkeys can choose in certain proportions as a general behaviour rather than finding one singular option as the optimum. (A) Payoff for monkey A in juice drops over 100 trials given proportions of choices of Monkey A on the x axis and monkey B on the Y axis. (B) Total payoff for both monkeys together in juice drops over 100 trials given proportions of choices of Monkey A on the x axis and monkey B on the Y axis. (C) Choice proportions for bins of 20 choices follow the payoff for both animals rather than payoffs for individuals. Dark blue indicate frequency = 0 which equates to no bins fitting that particular combination of choice proportions.

one animal the outcome for another animal is of course best as a single choice strategy, however a matched proportion can also yield an amount of reward close to the optimum (figure 6.7).

As the animals tend to swap between choice options quite a lot in the high temptation games it is interesting to look at the overall pattern of how animals match each other's probabilities and whether this can be explained based on the rewards that can be gained from these probabilities. This model of explaining proportional choice dependence is depicted in figure 6.7.

Strategies can be summarised as sets of rules that determine what the choice will be, given a set of circumstances. When classing trials as being played according to strategies all three strategies tested for could class a significant amount of trials. This is illustrated in figure 6.8. All confidence intervals of proportions are larger than by (50%) chance. The strategy that described the most trials, varied between animals and games.

Figure 6.8 – Behaviour according to strategies

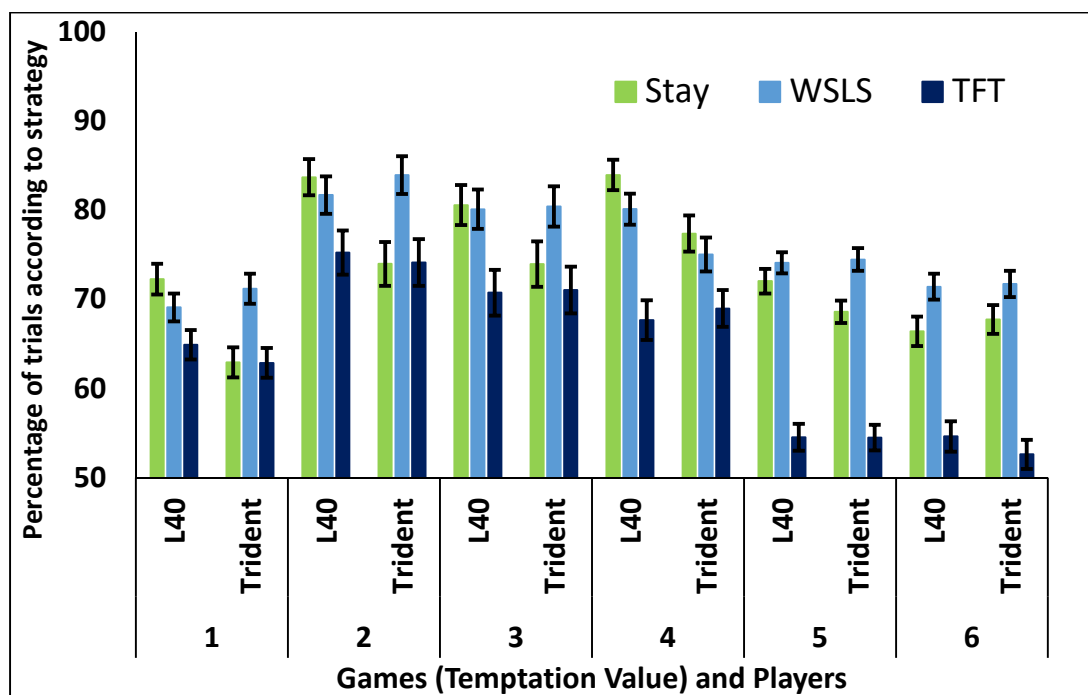


Figure 6.8 Three strategies were examined to classify behaviour by the animals. Persistence (Stay); Win-Stay Lose-Shift (WSLS) and Tit-for-Tat (TFT). All of these strategies would constitute 50% of trials if choice options were selected at random. All strategies can be used to classify a significant amount of trials in both animals and all games. WSLS tends to describe Tridents behaviour better in most games. L40 uses both persistence and WSLS more than TFT. For both monkeys behaviour according to TFT decreases in the cooperative games (Temptation=5-6) but this behaviour still remains above chance levels. Errorbars are 95% CI's.

Win-stay lose-shift strategy classifies significantly more trials than the Tit-for-tat strategy in both animals and all games. Especially in the cooperative games the amount of trials classed according to the Tit-for-tat strategy falls to between 53 and 55% of trials as compared to 63-74% of trials in the coordination games.

Figure 6.9 – Strategies in prisoners’ dilemmas increase odds of cooperation

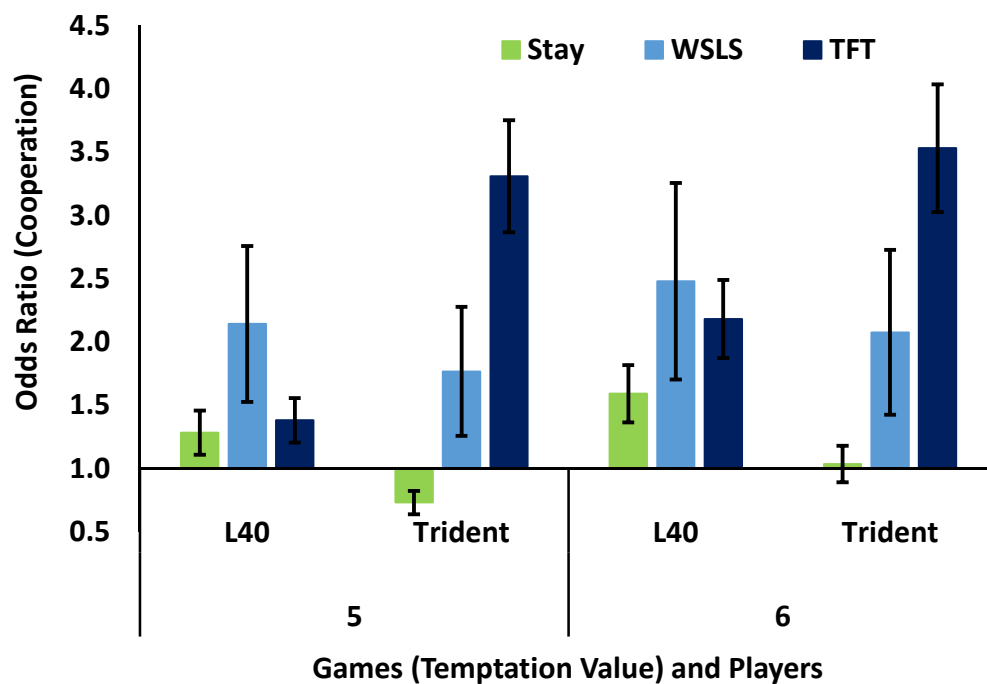


Figure 6.9 Strategies increase cooperation. An important question is whether monkey’s behaviour affects the outcomes of their choices. Here the relative odds of cooperation are plotted against the strategies. The odds ratios are the result of a comparison of the odds while the animals use a strategy versus when they do not use this strategy and therefore represent how effective the strategy is at increasing the odds of cooperation. Both WSL and TFT strategies increase the odds of cooperation in both cooperative games and in both animals. Persistence increases cooperation when performed by L40 but not when performed by Trident. Trident’s behaviour increases cooperation most when he behaves according to a tit for tat strategy.

Although the question of whether strategies occur is important, cooperation is our true object of interest. Thus, the more interesting question is whether strategies affect the odds of cooperation. To quantify this effect, logistic regressions were performed on cooperation with the three different strategies in separate models (equations 6.6-6.8). The odd’s ratio’s that were obtained are displayed in figure 6.9.

Use of information of the other's choices – The 'wall' control

To further investigate whether the monkeys use the information from the other's choices, a wall was used to obstruct the monkey's view of the other's choices. Comparisons of confidence intervals between conditions (figure 6.10) show that mutual choices for C did not decrease with the wall control in the coordination game. However cooperation significantly declined to below what one would expect to see by chance. In addition to this there is a dramatic shift from mutual cooperation to mutual defection when the animals no longer have access to the information of the other's choices. This was significantly less cooperation than in the open parts of these sessions.

Figure 6.10 – Decline of cooperation when animals have no access to other's choices

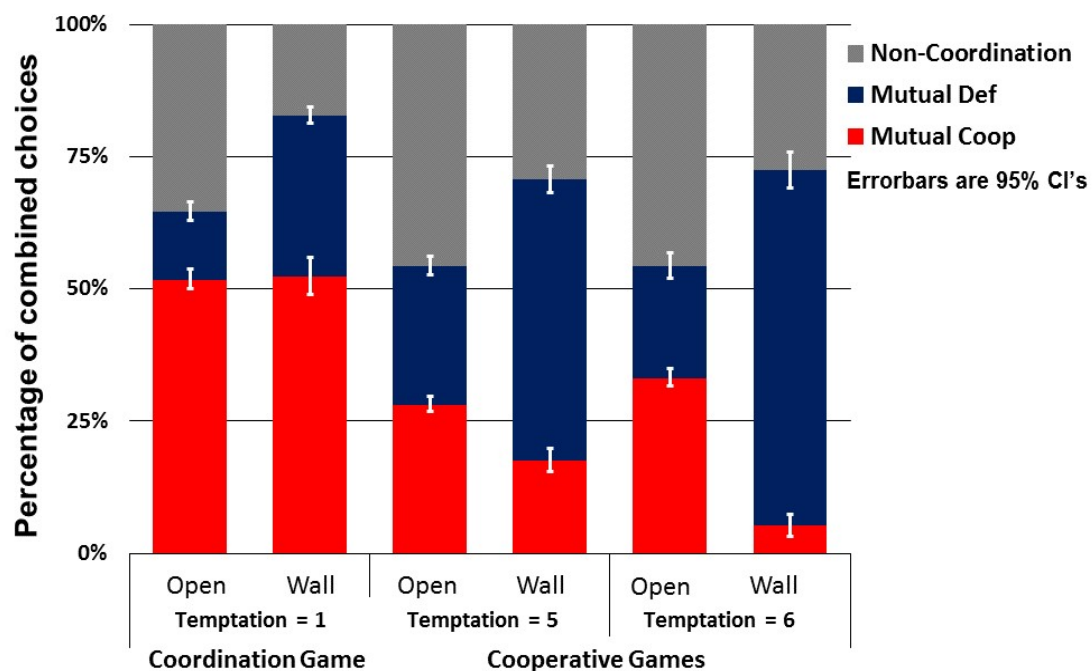


Figure 6.10 Playing games behind a wall. The wall obstructs information from the other's choices but nothing else. Mutual choices for C did not decrease with the wall control in the coordination game. However cooperation in cooperative games significantly declined. Noteworthy is that a shift from mutual cooperation to mutual defection takes place. Error bars are CI's. The error bars at the top of the blue bars are CI's of the cumulative red and blue to compare levels of coordination. Coordination increases in the wall control due to higher levels of mutual defection (or mutual D).

Strategies have been shown to have a positive effect on cooperation (figure 6.9). If this effect is dependent on the access to information of the other's choices, strategies should not have an effect on cooperation when playing behind the wall. I used a logistic regression on the occurrence of cooperation. A positive effect of strategies is seen on mutual choices for C in the coordination game

even behind the wall. However, as predicted, the effects of all strategies on cooperation become smaller or disappear when playing a prisoners dilemma in the wall control. Moreover, with a further increase in the temptation value, the strategies become detrimental to cooperation. This can possibly be explained by an increase in mutual defection which now will be the highest attainable option in many trials. This could possibly cause all strategies to focus on increasing choices for mutual defection rather than mutual cooperation.

Figure 6.11 - Strategies have a negative effect on cooperation in high temptation games

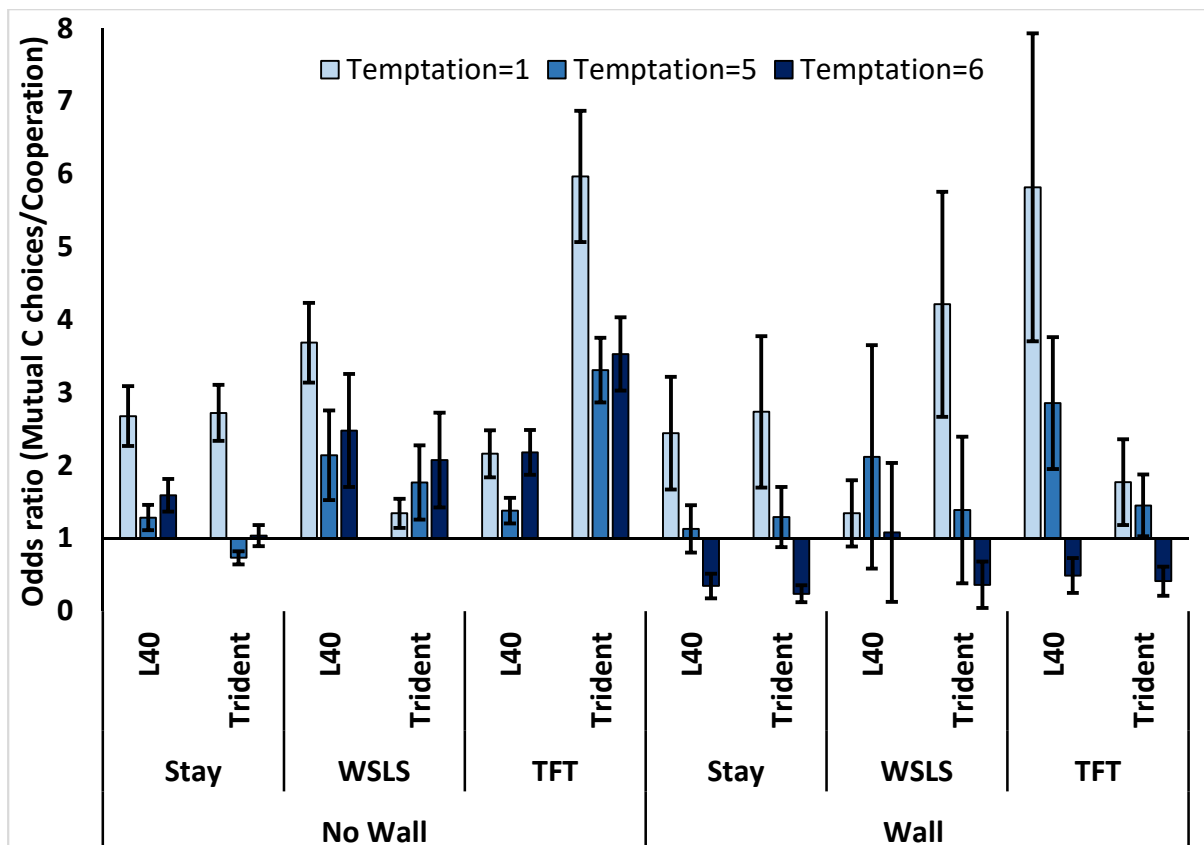


Figure 6.11 The effect of strategies on cooperation shifts when the animals cannot see each other's choices. Even though animals still behave according to strategies when a wall obstructs their view of the other's choices, it is the effect these strategies have on cooperation that changes. In the highest temptation value game the strategies even decrease cooperation.

Long term learning to cooperate

Cooperation is advantageous when it is played consistently over longer periods of time, this difference is subtle so may cause a long term reinforcement of this behaviour as it demands a memory of past trials. As coordination contains both mutual cooperation and defection it is relatively more rewarding trial by trial rather than over multiple trials like cooperation alone. If the

monkeys can integrate this subtle long term increase in reward of cooperation one would expect a long term learning effect of cooperation. Interestingly, when all trials in which cooperation games were played are numbered chronologically, the number of the trial has a very significant effect on its likelihood to be a trial in which the monkeys mutually cooperated ($p < 0.001$). Thus, the proportion of cooperation increases over time (figure 6.12, red). Coordination does not show this effect (figure 6.12, blue).

Figure 6.12 – Long term increase in Cooperation

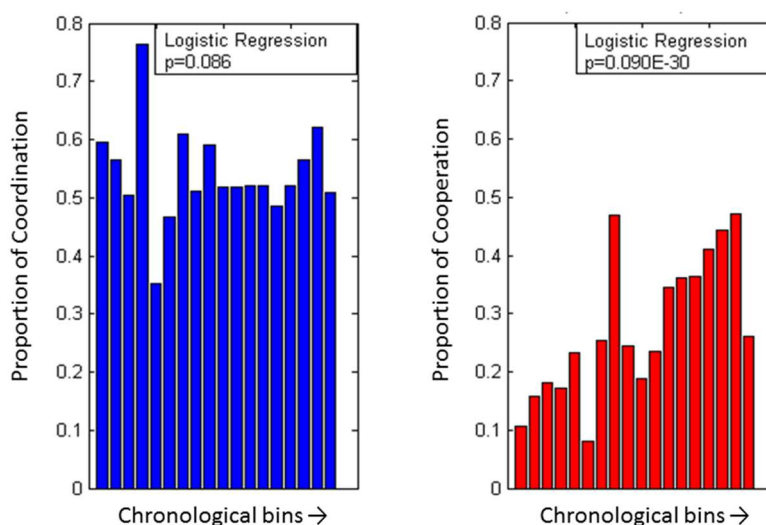


Figure 6.12 There is a long term effect of cooperation games on the proportion of cooperation. A logistic regression of the cooperation-trial number on the chance of cooperation shows that there is a significant increase in the likelihood of cooperation over time. The figures consist of even bins of data in all cooperative games in chronological order.

Conclusions and Discussion

‘Acting together’ versus ‘acting apart together’

In the experiment described in this chapter animals play six different games in which they choose between two options. Their rewards are dependent on the combined choices of both monkeys. The monkeys are allowed four seconds to both respond and can self-regulate which monkey goes first or second. Response-time analysis shows that the monkeys take turns to respond in the task on a number of trials resulting in trials where one of the monkeys has a slow reaction time whereas the other responds relatively fast. The differences between these responses are large on average and could indicate that the animals process the other’s response and take it into account. The animals seem to be playing the game together rather than acting alone. At the start of this dissertation I explained that the minimal social situation teaches us that cooperation can occur without any social

awareness. Noë also published a paper in 2004 that makes the point that cooperation can often occur in experiments by individual training on a task that then results in incidental cooperation. He also said that communication should be the emphasis of study (Noë, 2006). Even though I have not seen any evidence of communication (e.g. vocalisations) in the experimental setup relating to trial by trial behaviour, it is possible that monkeys watch what others do and adjust their behaviour accordingly. This is supported by the coordination shown in this dissertation and earlier publications of others (S. F. Brosnan, Wilson, et al., 2012; Bullinger et al., 2011; Mendres & de Waal, 2000). Taking turns is part of this behavioural adjustment to others.

Coordination and cooperation behaviour with access to other's choices

Monkeys cooperate even when they have access to the other's choices. It is reasonable to assume that access to the other's choices might have made players more vulnerable to exploitation and have made defection more frequent. As L40 is often the first to choose this may explain why Trident defects more often. However overall, there was still an above chance level mutual cooperation. Even though animals did defect when the other cooperated quite often, in the majority of trials where the first animal chose C the second animal still also choose C. This holds for all games and in both animals. Previous work by Haroush et al. used a prisoner's dilemma payoff scheme to look at encoding of other's choice predictions in neurons (Haroush & Williams, 2015). In this work, there was less mutual cooperation as animals individually showed higher proportions of defection. An important difference was that animals did not have access to the other's choices. This study is therefore more similar to the performance of the animals during the wall control. What is not clear is whether the animals in the study by Haroush et al. were aware that the choices of the other were actually generated by a real individual. In the experiment in this chapter the combination of turn-taking response times, coordination response times, conditional response times and the wall control all suggest the same thing. L40 and Trident were both aware of the other's choices and took the other's choice into account to make their own. Animals show a trial by trial faster response that seems related to both coordination and own reward. Whether reward or coordination are the drive behind the faster response this means that the monkeys are aware of the outcome of the trial which can only be known by an awareness of the other's choice. In humans it has previously been shown that cooperative choices are generally faster than non-cooperative choices (Rand & Nowak, 2013). This is consistent with my finding in macaques.

The effects of increasing temptation

In comparisons between games it is obvious that coordination with low temptation is quite stable while cooperation tends to break down regularly which makes the outcomes of the game more

volatile. Differences in levels of coordination and cooperation are larger between the coordination games and cooperative games than they are between the individual games within these classes. One could wonder whether the temptation value itself is less important than the binary class of the games. More analyses and model fitting would have to be done to answer this question.

One would expect that a larger temptation reward would result in even more defection and eventually would lead to cooperation failure. This is not the case within the range of games that I tested. The effect of strategies and effects of these strategies on cooperation are also only slightly smaller for 6 juice drops compared to 5 juice drops.

The only difference between the cooperative games arose when the animals could no longer use the other's choices in the wall control. In this control task, the monkeys played the game together with a short wall obstructing the view of the other's choices. In this control task, mutual cooperation becomes less frequent in the higher temptation cooperative game. In addition, the trials that are classed according to strategies no longer increase cooperation. In the highest temptation cooperative game, trials played according to strategies even become detrimental to the odds of cooperation. This shows that animals learned to cooperate in an environment where they could view the other's actions. Moreover, they became dependent on this information to cooperate. One final difference observed in higher temptation value games is that reinforcement learning values reduce in their predictive power of choices and cooperation. This means that higher temptation should result in more defection, but the animals actually overcome this obstacle. Thus, immediate rewards associated with the options are a less important factor to explain behaviour in high temptation games. Perhaps a compensation against the opposing valuation of options can account for the slight increase on cooperation seen in the highest temptation value prisoner's dilemma.

Alternating games may affect the choices in cooperative games. In humans setting a precedent for efficiency (coordination on an option that pays highest for all players) increases cooperation in a prisoner's dilemma (Knez & Camerer, 2000). This has never been shown before in monkeys but it is not inconceivable that monkeys also generalise certain behaviours from one task to another. If this effect was the only reason that the monkeys cooperated, I would have expected the cooperation to decline as monkeys play the game for longer. Quite the opposite occurred. Instead, monkeys cooperate more as they play the cooperative games for longer. It therefore seems unlikely that the cooperation is only due to the precedent that may have been set by a previous game.

Long term learning of cooperative action

As cooperation in the prisoner's dilemma is advantageous over multiple trials one would expect some learning to over longer periods of time in a dyad. Indeed this seems to be the case. While coordination stays stable within the game, cooperation steadily increases over time. Even though cooperation increases over time due to long term benefits of cooperation, coordination has immediate benefits to both animals and therefore does not require this long term effect to be established over time. As this was only measured in one dyad it will remain to be studied whether this increased level of cooperation remains or declines when these animals work with another third animal forming two new dyads.

Future Continuation

Given the results in this chapter, the first order of business is to finish this current project. A third subject has been trained (Virtue, as mentioned in chapter 5) to test the three subjects in the three different combinations to confirm the results so far. Furthermore, I would like to expand the analysis to study learning rates and the role of choice proportions in maximising reward. Ultimately, these experiments should lead to the contribution of a study which characterises macaque behaviours in different games. This enhanced understanding of macaque behaviour in social games could in turn inform future studies that aim to study social behaviour in the brain.

Chapter 7 – A step closer to understanding social behaviour in primates

Inequity attitude of Rhesus macaques

In this dissertation four separate but related experiments concerning inequity, social preferences, coordination and cooperation were discussed. From the results of some of these experiments it is clear that macaques observe inequity in their direct experimental surroundings and have behavioural responses to this parameter. Behavioural responses to inequity are not a novel observation, other studies have found that primates respond negatively to receiving less than conspecifics (S. Brosnan, 2006) and monkeys have been known to reject unequal payments (Sarah F Brosnan, 2009; Sarah F. Brosnan & de Waal, 2003). The behavioural responses (response times) we found for unequal reward stimuli were not consistent in their resulting conclusions on the topic of social preferences of macaques. The data contained a lot of variability from unknown sources and there may have been temporal effects that we were unaware of. A noteworthy observation is that in the study in which monkeys rejected unequal pay, this rejection did not remain stable over time. Indeed given enough repeated trials animals would accept the lower pay more often. Perhaps the fact that we recorded many sessions worth of trials in conjunction with individual differences in animal preferences contributed to our varied results and prohibits the recording of more varied natural behaviours that may only occur on a shorter time scale.

In addition to unaccounted for variability in data our data also seemed to suggest some counterintuitive results. Some of the response time analyses would seem to suggest that the monkeys preferred disadvantageous inequity and did not prefer advantageous inequity. This could possibly be a side effect of the way conditions were grouped and there may have been interactions between own reward and inequity effects on response times. More analyses would have to be done to confirm this possible explanation. Another potential explanation is that monkeys' social preferences depend on their own rewards as is confirmed by the choice data in chapter 4.

Did reciprocity and social closeness determine monkeys' inequity attitude?

When macaques play a choice task in which they choose between combinations of rewards for self and other it is apparent that at least one of the monkeys preferred to choose for the other monkey to have less reward but not in all conditions. I did not obtain enough data from the other monkeys to confirm whether this was also true in their cases. In this comparison all rewards for self were equal. In this task again Obi was the only acting monkey. Perhaps, reciprocity would have made a

difference in this behaviour. Reciprocity has long been known to be a characteristic of human interaction (Leventhal et al., 1969). It is conceivable that this was an important factor we didn't take into account. However the evidence for reciprocity in primates is not overwhelming. This was illustrated in a publication by Jaeggi et al. in 2013 that showed that when controlling for symmetrical long term relationships between primates there is no additional effect of reciprocity between grooming and food sharing (Jaeggi, De Groot, Stevens, & Van Schaik, 2013). This same work also illustrates another possible complication which is that the monkeys in one dyad were housed in different rooms. One can wonder whether the outcome would have been different if the monkeys were cage mates and interacted with each other more regularly. Social closeness has been observed to be related to heightened inequity tolerance of chimpanzees (Sarah F. Brosnan, Schiff, & de Waal, 2005). It is unknown whether this may also be the case for macaques, but it is possible.

Combined choices, can rhesus macaques work together?

Considering that (our specific) macaques do not seem to have pro-social inequity preferences, it is possible that this would make it hard for monkeys to cooperate. It has been suggested that inequity aversion "improves the prospects for voluntary cooperation" in humans (E. Fehr & Schmidt, 1999). In the work presented in this thesis I did not find sufficient evidence to support whether this is the case in our monkeys. Inequity attitude has not clearly been defined in any of the animals. In addition to this, cooperation has only been studied in one pair of animals. Despite this inability to draw firm conclusions our monkeys were able to coordinate their actions and cooperate. The games that monkeys played in my study show some similarities with studies that have been done before. Coordination has been studied in capuchins, macaques, chimpanzees and humans using a 'stag hunt' or assurance game (S. F. Brosnan, Wilson, et al., 2012; Bullinger et al., 2011). This game is analogous to my design where the temptation is 2 drops. The interesting thing about this task is that there is a safe option that always pays two regardless of the other, and a risky option that pays four but only if both animals go for it. Our macaques coordinate on the higher option about 60% of the trials, this is slightly lower than seen in other stag hunt games played by macaques, however the game in this paper was only played with one set of stimuli and therefore animals were able to converge on an option and learn over many trials. In my design animals are required to learn new stimuli many times which creates more error. I could have removed a part of the data from the start of a new fractal set, but I did not wish to make any assumptions about how quickly the animals learned the payoffs for new images. There has also been a study using cooperative games which used a prisoners dilemma (Haroush & Williams, 2015), this study used a payoff scheme similar to my prisoner's dilemma with 6 juice drops for temptation and found only 17.1% mutual cooperation. The animals managed to coordinate in this task by choosing C mutually more than expected from their individual

probabilities. What is not well understood is whether the monkeys in this task are aware of the other actor and whether they would have cooperated more if they had access to the other's choices while performing the trials. What my study has to offer is that I show that monkeys use the information of the other's choice when given this option and that this increases cooperation. This is consistent with the study by Haroush and Williams in which monkeys did not have this information available.

Reward and punishment

Since there are practical and ethical issues to consider when performing experiments that use punishments; most studies that look at games in the last decades have focused on training through rewards. In the minimal social situation (discussed in chapter 1) for example, there was more cooperation when using punishments rather than rewards (Sidowski, 1957). It could very well be that studies that look at social behaviour with a focus on rewards are missing an important part of why these behaviours evolve. The truth is that cooperation in humans may often take place under threat of violence or punishment under influence of negative emotion induced by free riders (Ernst Fehr & Gächter, 2000). A large meta-analysis on the contributing factors for cooperation also showed that both rewards and punishments can contribute to cooperation (Balliet, Mulder, & Van Lange, 2011). In the experiments presented here, given that they have information of the other's choice, I initially expected that the monkeys would use the opportunity to defect more than they did. However, they very steadily keep choosing cooperation, even when they receive only one drop of juice at times. Perhaps receiving smaller reward is not enough of a deterrent from risking cooperation. Based on other research, perhaps an aversive stimulus would show a much more likely behaviour of defection as the penalty for unilateral cooperation could be highly aversive. If higher levels of defection arise, there may also be a much slower learning of the benefits of cooperation as this would be less often experienced. This 'negative spiral' has not previously been discussed but it could intuitively contribute to more stable behaviours over time. More analysis and modelling would have to be done to confirm whether this would be the case. Importantly, performance could look different if unilateral cooperation consisted of a negative stimulus like an air puff. It is important to keep this in mind if comparing this result to other studies where negative stimuli are used.

Limitations of an experimental rather than a natural context

It is important to note that there are limits to how we can translate experimental data from macaques to not only humans but even to natural macaque behaviour for several reasons. The animals are water restricted which makes them eager to perform a large amount of trials which they would otherwise not do. It would be inaccurate to say that this is the only reason they perform the

tasks. Experience in working with several macaques has taught me that these animals in some cases continue to perform trials for large amounts of juice past the amount that they would drink when offered it for free. This leads me to believe that performing the tasks is in fact an engaging enrichment to the animals. In addition to their water restriction, the reward structures we use, presenting them with small discrete drops of juice, would be encountered nowhere in a natural setting. One could expect animals to possibly respond differently when bigger rewards are at stake or if they were already saturated. In this dissertation no analysis was done or presented on how saturation may affect the results. In future studies and continuation of the projects this should be analysed as animals can be expected to be more saturated towards the end of sessions and this could be used to answer questions surrounding this.

Animals are trained for many sessions in advance which allows the animals to establish behaviours which are recorded as data. For instance, when presented with a task on the screen the animals will perform the task as they will make a choice between options knowing that they will receive a reward regardless of whether they know what the stimuli mean. What is clear is that in the pair of animals we tested so far, cooperation increases over time. It is not clear whether this increase comes from an increased willingness to cooperate with their partner (social reasons) or an increased understanding of the task. Hopefully repeating this analysis in a pair of animals in which one animal is new to the task and the other is not will answer this question as we would expect animals to have to re-establish levels of cooperation in this case if it were a social effect. Whereas, if they simply learn the payoff structure and do not factor in the social context, they will continue their high levels of cooperation no matter what the behaviour of their new partner is.

Despite the limitations in our methods and the restrictions these offer with regard to what we can say about natural behaviours of macaques and humans there are also certain strengths to our methods which allow us to distinguish behaviours that would otherwise remain unclear. By staying within a small range of rewards we allow for little variation between conditions. Unlike a natural setting where, for instance, changes in animal identity, proximity, reward magnitude and identity can influence outcomes, in the experimental settings all of these factors are controlled which means we can attempt to study the isolated variable of interest. Also, even though our results only limitedly inform natural behaviours, they more greatly influence what we can conclude from neuronal recording studies which are conducted in more similar ways to these experiments. This is of great importance as given the cost and ethical implications of recording from primates, this data is precious and should be used to its full potential. If we can understand behaviours performed in the

lab to the best of our abilities, this will greatly improve the conclusions and implications of recording studies performed under similar circumstances.

In addition to limitations caused by the reward structure and iterative nature of our tasks, the animals are not allowed to choose their partners in the social experiments which may give rise to differences with how animals would behave naturally. Both macaques and humans determine to a large degree who they interact with. For instance the animals could be more naturally inclined to cooperate if there is more social closeness, relatedness or if there is a particular dominance relationship between the animals. Because we only have data from a couple of animals we cannot say anything conclusive about how dominance or social closeness affected our experiments however this has been studied by others in past years.

Dominance, inequity and cooperation

Social hierarchies have been shown to affect brain activity in humans (Zink et al., 2008) and primates (Santos, Nagasaka, Fujii, & Nakahara, 2012). Cooperative feeding or food sharing has been described to be less common in despotic species like macaques (Dubuc, Hughes, Cascio, & Santos, 2012) and more common in dominant than in submissive animals within these groups (Massen, van den Berg, Spruijt, & Sterck, 2010). Part of this can possibly be explained by modulation of competition and cooperation by social states in dominance hierarchies. Striatal activity has previously been studied in an experiment in which animals were required to compete for (grab) food against a dominant competitor (Santos et al., 2012). Results showed that neurons in the caudate nucleus which were involved in responding to the reward were less active when the monkeys were in a submissive state. As our monkeys were not required to compete for rewards or respond to another monkey it seems unlikely that this would affect the overall results for an individual animal. However, it could, in part, explain why there are such large differences between the animals. As animals partially grow up in our groups, social dominance shifts do occur. Although we did not observe any large shifts during our experiments, this does not preclude that there may have been more subtle shifts in the submissive state of the animals in relation to each other or even on a day to day basis. In our current data we have no way to take this into account at this current moment. However, for future experiments, it may be good to develop an assessment of social dominance before every session so that we can control for this.

My contribution to science and future aims

In this dissertation I have shared a summary of four years of work. First I studied inequity and discovered that inequity behaviour in macaques is hard to characterise. However, as a result of this

study we discovered that striatal neurons encode own rewards, but are also modulated by disadvantageous or advantageous inequity (Báez-Mendoza et al., 2015). The next two years of my PhD candidacy was spent designing and performing a behavioural study on combined choices. With the results that I have gathered so far, it is clear that macaques can coordinate to gain higher rewards and that they can improve this coordination by acting according to strategies. When varying the task between simple coordination games and cooperative games, the animals show marked changes in behaviour related to the game they play. Mutual choices for the pareto-efficient option (cooperation) occurs less in prisoner's dilemmas but are not abolished. In fact, the amount of cooperation is above what one would expect by chance which is higher than found in other studies. Amongst other differences the monkeys also show different patterns of strategy. As the games result in reward differently. Importantly, my data shows that macaques also use information from the other's choices as shown with a control in which views of the other's choices were blocked.

After we have done a satisfactory deliberation on cooperative behaviour, it would be interesting to start exploring how brain activity relates to this behaviour and the processing of social decisions. The fact that macaques can use the information from others is very reassuring that other's actions may have reinforcing effects and could possibly also be represented in own action values. It is the combination of behaviour and neuronal recordings that will eventually teach us how the brain computes and regulates social behaviour. Ultimately, this work will help us understand social behaviour.

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