Visual attention and cognitive performance in sheep

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Abstract

Cognitive probes are increasingly being used as an inferred measure of the emotional (and thus welfare) status of the animal. This reflects the bidirectional and interactive nature of emotional and cognitive systems. To date, cognitive paradigms have focused on how the emotional system biases expected outcome of prospective actions within goal-orientated scenarios. Evidence, however, suggests that negative affective state can also modulate attentional mechanisms. Measuring attention alongside other current tests of cognitive bias may provide greater resolution in the measurement of animal welfare. As a starting point for developing cognitive tasks of attentional control, we decided to assess the basic relationship between visual attention and cognitive performance in a farm animal species (sheep).

Variation in visual attention and cognitive performance was sought through testing of four different breeds of upland and lowland sheep (Beulah, Blue face Leicester, Texel and Suffolk; n=15/ breed) on a visual attention task and a two-choice visual discrimination task (to measure cognitive performance).

Cognitive performance and visual attention differed significantly between breeds ($F_{3,46}$=4.70, p=0.006 and $F_{3,5o}$=6.05, p<0.001 respectively). The least visually attentive breed of sheep (Blue face Leicester) had the lowest level of cognitive performance and the most visually attentive breed (Suffolk) had the highest level of cognitive performance. A weak but significant relationship between vigilance/fearfulness and visual attention was also observed (t_{44}=3.91, p=<0.001; r^2= 0.23) that appeared to adhere to the Yerkes-Dodson law, with both high and low levels of vigilance/fearfulness having a negative effect on visual attention. These results demonstrate a discernible relationship between visual attention and cognitive performance that provides a basis for further exploring attention systems in the context of changes in animal affective state and thus animal welfare.

Introduction

Cognitive probes are increasingly being used as an inferred measure of the emotional and thus welfare status of the animal (Harding et al., 2004; Burman et al., 2011; Gygax, 2014; Hales et al., 2014; Baciadonna and McElligott, 2015; Roelofs et al., 2017). This reflects the bidirectional and interactive nature of emotional and cognitive systems (Banich et al., 2009) where the emotional system is considered to bias the expected outcome of prospective actions within goal-orientated scenarios. Emotional state biases can however affect cognition in ways other than shifts in expected outcome. For example, substantial evidence suggests that attentional mechanisms (and thus cognition) are also highly affected by negative affective state (Eysenck and Derakshan, 2011). Referred to as attentional control theory, bias can occur due to an imbalance between goal-directed and stimulus–driven attentional systems where a negative affective state weakens the former and strengthens the latter to produce a lack of attentional control (Richards et al., 2012). The lateral intraparietal region of the brain appears to be central to these competing attentional mechanisms and is often described as the brain's multimodal priority map (Gottlieb, 2007). Fronto-parietal networks have the ability to steer attention towards current executive goals, but the parietal region is highly influenced by the emotional state of the subject (Viviani, 2013). For example, individuals with depression, anxiety and negative mood state focus significantly more on negative or threatening stimuli in their environment, supporting the idea that attention is guided not only by the external context but also by the internal state of the individual (Joormann and Arditte, 2013). Attentional bias can thus have a detrimental effect on accurate and efficient cognitive processing and tests that can monitor this type of cognitive disturbance are thus potentially pertinent measures of affective state (Joormann and Siemer, 2011). It follows, therefore, that cognitive tests of judgment bias may in fact be measures in shifts of attention or, there may be a complex and integrated effect of judgement and attention bias on cognitive performance. From a practical perspective, the relationship between judgement bias and attention may be important. If these attributes correlate, then one measure is will be as useful as the other in measuring the affective state (Figure 1a). However, there may also be a more complex relationship between affective state and attention which has the potential to identify additional affect phenotypes (Figure 1b). For example, animals experiencing emotions of negative valence may be in different affect states that can only be discriminated by also assessing the level of visual attention (Figure 1b). These states may be similar to what has previously been proposed by Mendl et al. (2010) e.g. anxiety versus behavioural depression (Figure 1c). Thus, measuring attention alongside other current tests of cognitive bias may provide greater resolution in the measurement of animal welfare

As a starting point for developing cognitive tasks of attentional control (as inferred measures of affective state), we decided to assess the basic relationship between visual attention and cognitive performance in a farm animal species, sheep. Domestic selection has led to reasonable interbreed variation in vigilance/fearfulness between sheep breeds and thus potentially visual attention. For example, upland sheep are more prone to predation and need to be capable of locating areas of shelter as well as grazing and water sources, thus may be more vigilant and attentive to changes in their environment, particularly in the context of protecting young (see Dwyer and Lawrence, 2005, for review). By contrast, lowland breeds tend to be managed more intensively in a way that actively deters natural predators with shelter food and water being consistently provided. Consequently, lowland breeds may have lower fearfulness/vigilance levels by comparison and be less visually attentive. The aim of the study, therefore, was to examine the relationship between visual attention and cognitive performance (in a two-choice discrimination task) using four different upland and lowland breeds of sheep.

Experimental Procedures

Animals

Four different types of female lowland and upland sheep (Bluefaced Leicester (lowland)(N=15), Texel (lowland, island) (N=14), Suffolk (lowland) (N=14) Beulah (upland) (N=14) Table 1) randomly selected from pure-bred flocks were used in the study. All animals were 9 months old and born and maintained within the same lowland husbandry system at Aberystwyth University. Prior to the study, all animals lived outdoors and each had received the same amount of handling as part of the routine husbandry. During the study, all animals were kept indoors in a university stock barn with *ad libitum* water and hay. Animals were kept in their new group composition and indoor housing for seven days before training and testing commenced. All animals were given a daily feed supplement in the form of a standard ration of 400g cereal-based pelleted concentrate per day (Wynstay Lamb Finishing nuts, Wynstay, UK). On testing days, these pellets were provided as the food reward within the operant task (see below). Studies were carried out in accordance with the UK Animals (Scientific Procedures) Act, 1986. All animals came from permanent stock flocks held at Aberystwyth University where the experimental work was carried out. Animals were returned to the stock flocks on completion of the study.

Vigilance/Fearfulness Testing

The four breeds were initially group-tested to confirm general variation in vigilance/fearfulness and thus potentially visual attention. Both tests were carried out once a day at 09:00h for 6 days. This time point was the first of two normal feeding times for all sheep. The first test (Trough test) involved placing food in a 3m food trough within the animals' normal husbandry enclosure whilst the human observer stood at the mid-point of the trough (Figure 2a). Over the course of 5 minutes the number of animals that ate from the trough was recorded. The second (Chair test) involved the human observer seated on a blue fold-up chair within the animals' normal husbandry enclosure. A bucket (yellow), from which animals were normally fed, was placed between the observer's legs (Figure 2b). Over the course of 5 minutes, the number of animals that ate from the bucket was recorded.

Operant system

We used a purpose-built semi-automated operant system for the cognitive testing (McBride et al., 2016). This system consists of an ambulatory one-way circuit within an arena (8.7 x 3.1m) in which animals engage and then disengage with the visual stimuli during each trial (Figure 3). The semi-automated nature of the system is controlled via diffuse-reflective photo-electric sensors (Omron, Nufringen, Germany), Matlab R2015a (Mathworks, UK) in conjunction with Psychtoolbox (Psyctoolbox.org) and a 12 bit USB data acquisition device (DAQ; MCC 1208fs; Measurement Computing, Norton, USA). Visual stimuli are presented via liquid crystal display (LCD) screens (1280 x 1024 pixel resolution, 250cd/m2 Brightness)(Dell, UK) and the reward (5g of normal sheep ration in the form of pellets) is delivered into a trough directly underneath the screens via an in-house designed feed dispenser (Quality Equipment, Woolpit, UK).

Acclimation and Training in the Operant Testing System

In the acclimation phase, animals were habituated to the operant testing system. Animals were fed pellets from buckets randomly located in the operant system, first as a single group (1 x 15 minute session), then as sub-groups of 7-8 (2x 15 minute sessions) and then groups of 3 (1 x15 minute sessions). Finally, animals were fed as pairs within the system (except for one group of Bluefaced Leicester sheep that was maintained as a group of 3 due to the total number for this group [15]), with pellets dispensed from the feed-dispenser (1 x15 minute sessions) remotely controlled by the operator.

All animals progressed singly through three stages of training to use the operant system as previosuly described (McBride et al., 2016). In brief, stage 1 training involved the simultaneous presentation of random images (Wingding font; Microsoft, USA) on both screens, with presentation of the food reward in both feed troughs and simultaneous presentation of an audible tone (750Hz, 0.5s). The tone was used to create a conditioned stimulus (cue) for the presentation of the stimulus. Stage 2 training presented a single image on one of the screens with simultaneous presentation of the audible tone (750Hz, 0.5s). This required the animal to move towards that screen in order to receive a food reward. Stage 3 training introduced the one-way ambulatory circuit and also required the animal to choose the screen on which the single image was presented (with simultaneous presentation of the audible tone (750Hz, 0.5s)) in order to receive the food reward. Choosing the incorrect screen elicited no food reward but the animal was able to move directly to the correct screen in order to elicit the food reward. These three training stages had the purpose of i) habituating and positively conditioining the animal to work in the operant system by themseleves, ii) promoting trial and error behaviour between the two points of reward delivery, and iii) introducing the animals to the one-way ambulatory circuit within each operant trial. Groups of animal received 1 training session per day with 3-9 sessions of Stage 1 training, 4 sessions of Stage 2 training and 3 sessions of Stage 3 training.

Measurement of visual attention

The visual attenion task involved the presentation of a single stimulus on one of two screens. Sheep were require to be attentive to the visual stimulus and choose the screen with the image in order to elicit a correct response and a food reward. For each trial, one visual stimulus, randomly chosen from a library of 10 wingding images, was presented on one screen (pseudorandomly; 50% left, 50% right, position 1 and 2, Figure 3) with simultaneous presentation of an audible tone (750Hz, 0.5s). An incorrect choice led to the presentation of a high pitched audible tone (1000Hz, 0.5s), the image being removing and the animal being required to reinitiate the trial by moving back through the ambulatory circuit . Each session constituted 10 trials and the number of correct trials (animals choosing the single stimulus) was recorded over 4 sessions. If an animal did not respond to the visual stimulus within 3 minutes, the trial would time out and the next trail would commence after the animal passed through the central corridor of the operant system.

Two-choice visual discrimination task

The two-choice visual discrimination task consists of the concurrent presentation of two visual stimuli (A, B), one of which is assigned as the S+ (reward presentation) and one of which is assigned as the S- (no reward). Stimuli were presented concurrently on two screens (pseudorandomly; 50% left, 50% right, position 1 and 2, Figure 3) with simultaneous presentation of an audible tone (750Hz, 0.5s). For half of the subjects (pseudorandomly allocated), stimulus A was the S+. For the other half, stimulus B was the S+. A correct response elicted a food reward and an incorrect response resulted in the presentation of a high pitched audible tone (1000Hz, 0.5s) and no food reward. An incorrect response also resulted in the animal moving onto 'correction' trials (a repeat of the the incorrect trial) until a correct reponse was given. Correction trials prevented strategies of a side-bias whereby the animal would consistently choose one side in order to attain 50% of the total reward (Horner et al., 2013). Each trial was time-limited to 45 seconds after which a high pitched audible tone (2250Hz, 0.3s) was sounded and the trial ended. Each session consisted of 10 trials (stimuli presentations). The end of the session was indicated by a prolonged low-pitched audible tone (260Hz, 1.9s). The learning criterion was set at either 6 consecutive ($p=0.015$) or 9 out of 10 ($p=0.01$) correct responses. Animals continued on the acquistion learning phase until they reached criterion (Acquisition 1). Once animals had reached criterion for the first acquisition, they moved to the reversal phase (Reversal), where S+ and S- were reversed. If animals did not reach learning criterion after 100 trials (10 sessions) during the frist acqusition, they were removed from the trial. Animals continued on the reversal learning phase until they met criterion. The animals then performed a third and final phase where a second set of novel stimuli were presented (Acquistion 2).

Statistics

In order to confirm statistical variation in the level of vigilance/fearfulness between breeds, the total number of animals per breed that approached the trough and chair over the 6 sessions was compared statistically using a chi-squared test. This analysis gave a vigilance rank (1-4) for each breed. Repeated measures ANOVA was also used to assess the difference in responses between the two tests over the six exposures (with Breed set as Block).

Visual attention data were the total number of correct responses during the session giving one value per sheep per session (for 4 sessions). Cognitive performance data were the number of trials taken to reach learning criterion for each sheep for each of the 3 phases of the cognitive task (Acquisition 1, Reversal, Acquisition 2).

The underlying assumptions necessary for parametric statistical analysis (normality and equal variance) were confirmed for both the visual attention and visual discrimination-reversal data sets. To establish the effect of breed on visual attention, data were analysed using repeated measures ANOVA with breed set as the between-subjects factor and session set as the within-subject variable. Post-hoc analyses between individual breeds was performed using the Bonferroni test. Each phase of the cognitive test was treated as a separate measure (Chase et al., 2012).

To establish breed variation within each phase of the cognition task, data were analysed using one-way ANOVA with breed set as the between-subjects factor. Post-hoc analyses between individual breeds was performed using the Bonferroni test.

In order to assess whether vigilance levels were predictive of visual attention, a linear regression with groups analysis was carried out using the vigilance rank and the number of correct responses during the first stage of the visual attention data (response variate: first stage of the visual attention; explanatory variate: vigilance rank; final model: parallel lines, estimate lines).

Linear regression with groups analysis was also used to quantify the relationship between each of the visual attention data (stages 1-4) and the visual discrimination-reversal data (3 phases). (response variate: each phase of the cognitive task; explanatory variate: each stage of the visual attention data; final model: parallel lines, estimate line).

All statistical analyses were carried out using GenStat , 16^{th} Edition . Statistical significance was set at $p=0.05$. All data are presented as mean±SEM.

Results

Confirming general variation in vigilance/fearfulness

There was a significant difference between breeds for both the Trough (d.f.= 3, χ^2=41.01, p<0.0001) and the Chair test (d.f.=3, χ^2=82.74, p<0.0001) test, thus confirming a range of vigilance/fearfulness levels over the four breeds (Figure 4a, 3b). The overall vigilance/fearfulness rank from high to low was Beulah>Suffolk>Texel> Bluefaced Leicester . Fewer animals from all breeds approached the human operator during the Chair test (where the human operator faced the sheep) than for the Trough test (where the operator had his back to the sheep) ($F_{1,30}$=7.6, p<0.028).

Variation in visual attention

There was a significant effect of breed on the number of correct choices made in the four visual attention sessions ($F_{3,50}$=6.05, p=0.001). There was no significant interaction with time (Stage) and thus post-hoc comparisons were not be made on per stage basis. Overall, Suffolk sheep made significantly more correct responses compared to Texel (8.11±0.44 versus 6.32 ±0.43 trials; p=0.032) and Bluefaced Leicester (8.11±0.44 versus 5.58 ±0.41 trials; p=0.001) and approached significantly more correct responses in comparison to the Beulah sheep (8.11±0.44 versus 6.48 ±0.46 trials; p=0.083) (Figure 5). Finally, there was a weak but significant regression between the vigilance rank of the four breeds of sheep and the number of correct responses during the first session of the visual attention data (t_{44}=3.91, p=<0.001; r^2= 0.23).

Variation in cognitive ability

Out of the 57 animals tested on the visual attention paradigm, 55 proceeded to the two-choice visual discrimination paradigm due to 2 Beulah sheep becoming too reactive within the operant system. Five sheep (2 Texel, 2 BF, and 1 Suffolk) exceeded the 100 trial (10 sessions) limit during the first acquisition and thus did not proceed to the second or third phase of the two-choice visual discrimination test. One Beulah and 1 Suffolk sheep stopped responding during the first acquisition phase (after 77 and 46 trials respectively) and did not proceed with the remainder of the cognitive task.

There was no effect of breed on the number of trials required to reach the learning criterion during Acquisition 1 (Figure 6). There was, however, a significant effect of breed on the number of trials needed to reach criterion during the Reversal phase ($F_{3,46}$=4.70, p=0.006) with the Bluefaced Leicester sheep requiring significantly more trials than any of the other three breeds. There was a significant effect of breed during Acquisition 2 ($F_{3,46}$=5.04, p=0.004) with Bluefaced Leicester sheep also requiring significantly more trials to reach criterion compared to the other three breeds.

Correlation between visual attention and different phases of the two-choice visual discrimination task

The correct number of responses from the first session of the visual attention data did not significantly regress against the performance data (number of correct responses all three phases of the two-choice visual discrimination task). Visual attention data for sessions 2-4, significantly regressed against the Acquisition 1 data (Session 2, t_{43}=-317, p<0.003, r^2=0.25; Session 3, t_{43}=-2.8, p<0.027, r^2=0.17; Session 4, t_{43}=-3.45, p<0.001, r^2=0.27).

No other significant regression associations were reported between the visual attention and cognitive performance data.

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Discussion

There was significant variation in vigilance/fearfulness (as measured via the trough and chair test) between breeds. It was anticipated that upland sheep would be the most vigilant breed of sheep because they have been selected to survive within highly demanding husbandry environments. This was indeed the case, with the Beulah sheep ranked 1 for vigilance/fearfulness. The three lowland breeds of sheep demonstrated variable levels of vigilance/fearfulness (Suffolk>Texel>Bluefaced Leicester) thus providing a range upon which hypotheses about visual attention and cognitive performance could be developed and tested. Interestingly, although there was a significant relationship between vigilance/fearfulness rank and visual attention, the two variables did not correspond completely. Beulah sheep were the most vigilant but were only on the second most visually attentive breed of sheep. Suffolk sheep had the highest levels of visual attention throughout the four sessions of the visual attention test, but were ranked second for vigilance/fearfulness. Although based on a small number of phenotypes (4), these data are suggestive of the Yerkes-Dodson law (Yerkes and Dodson, 1908), where high levels of arousal have a negative effect, either directly or indirectly, on visual attention. High levels of anxiety have been shown previously to reduce the efficiency of visual attention (Janelle et al., 1999). This is thought to be due to a more eccentric gaze resulting in more fixations and saccades towards both relevant and irrelevant peripheral stimuli. Although the Janelle et al. (1999) study was in humans, heightened eccentric gaze during high vigilance/fearfulness states would have evolutionary advantage for a prey species by increasing the chances of predator detection. Visual attention in this context would not necessarily be diminished, but rather might be spread less efficiently over a wider egocentric gaze space. Thus, in visual-based paradigms where the salient visual cues are located proximally, heightened vigilance/fearfulness may be disadvantageous. The reverse may also be true in visual paradigms where visual cues are presented distally, for example in maze tests (D'Hooge and De Deyn, 2001). This is an interesting and testable hypothesis for future cognitive studies particularly if it could be assessed across a range of prey to predator species.

On examining the relationship between visual attention and cognitive performance, we found a complex relationship between these two attributes. The analysis demonstrated that, while the first session of the visual attention test was not predictive of performance within all three phases of the cognitive task, sessions 2-4 of the visual attention test were predictive of performance within first phase of the cognitive task (Acquisition 1). These data may suggest different forms of visual attention with a form of innate or basal level visual attention being measured during the first session of the visual attention test, and a learnt form of visual attention representing the incremental increase in visual attention during subsequent test sessions (2-4). In terms of the cognitive test, the initial acquisition phase of the two-choice visual discrimination task recruits fundamental processes of associative rule learning, whereas the reversal phase requires the breaking and re-establishment of associative links related to rule change (Roberts et al., 1988). The second acquisition phase involves attentional set shifting. This is the disregarding of prior information in order to establish a new set of associative links (Bissonette et al., 2013). Learnt visual attention may thus only be predictive of performance during the first phase of the cognitive task (first acquisition). This may suggest a commonality of simpler associative learning processes that do not extend towards the more complex mechanisms associated with the last two phases of the cognitive task. Interestingly, this differentiation between the various phases of the two-choice visual discrimination task is supported by data from neurophysiological studies in which lesioning of the orbital frontal cortex in rats impairs the reversal and/or second acquisition phases of an intra-dimensional set shifting task but not the initial acquisition (Chase et al., 2012).

Conclusion

The data showed a significant relationship between vigilance/fearfulness state and visual attention data with results pointing towards the Yerkes-Dodson law (Yerkes and Dodson, 1908) whereby both high and low levels of vigilance/fearfulness reduced levels of visual attention. The data also hinted at two types of visual attention, innate and learnt. Learnt visual attention may share some simple associative learning processes that underpin initial acquisition during the cognitive task but appears to lack commonality with the more complex mechanisms of re-learning and set-shifting. Overall, these data suggest that shifts in visual attention have the potential to affect cognitive performance. This work provides a starting point to assess visual attention and judgment bias concurrently across a range of different affective states in order to assess their combined or independent effects on cognitive performance. This may provide a method of finer resolution in the assessment of animal affective state (and thus animal welfare).

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Conflict of interests:

The authors declare that they have no conflict of interest. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

Ethical approval:

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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Figure Descriptions

Figure 1. Hypothetical relationship of visual attention with valence state. **a.** a simple linear relationship between attention and emotional state (positive and negative valence) suggesting a joint underlying mechanism; **b.** a more complex relationship between attention and emotional state controlled by independent mechanisms that may interact; **c.** core affect represented in two-dimensional space (adapted from Mendl et al., 2010).

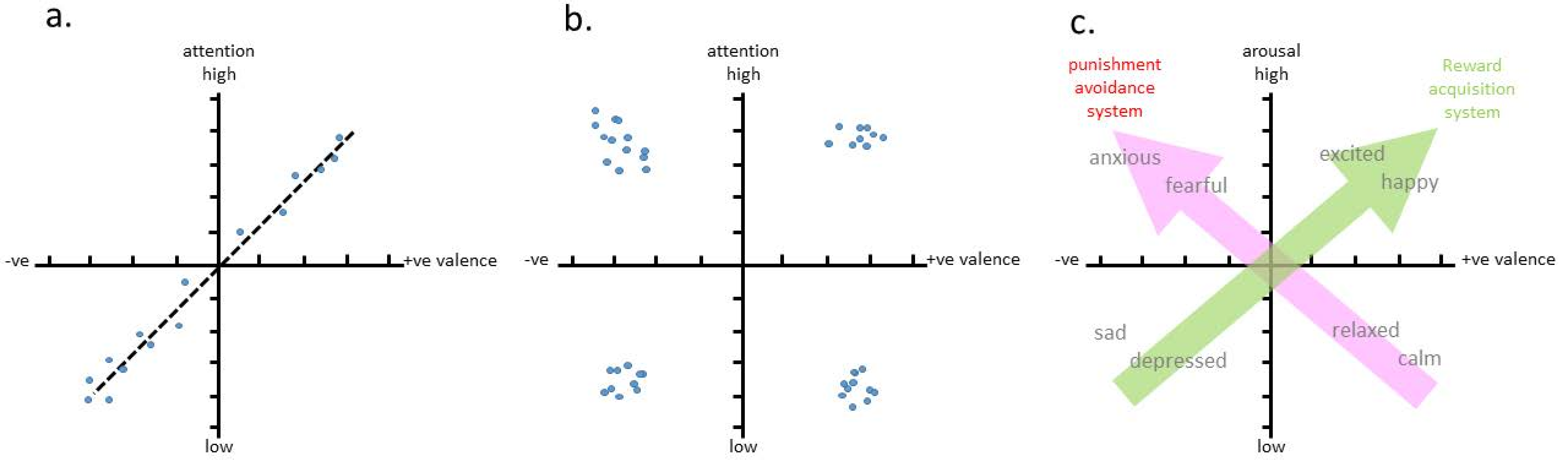
Figure 2. The Trough (A.) and Chair (B.) test to measure vigilance/fearfulness in sheep. In the Trough test, the human operator stood at the midpoint of the trough with his back to the animals. In the Chair test, the human operator sat on a seat in the middle of the pen with a yellow bucket between his legs.  Human observer;  Yellow bucket.

Figure 3. A diagram of the operant system. Within each trial, a sheep travelled the ambulatory circuit to make a choice in the stimulus-reward area.

Figure 4. A pictorial illustration of the results from the start, middle and end of the human fearfulness tests (trough and chair) (sessions 1, 3 and 6) (BFL-Bluefaced Leicester).

Figure 5. The mean number of correct trials during the four sessions of the visual attention task for four breeds of sheep (Bluefaced Leicester, Texel, Suffolk and Beulah). Data are mean ± SEM. Pairwise comparisons are between breeds across all four sessions; * $p<0.05$, ** $p<0.01$, $p<0.001$.

Figure 6. The mean number of trials to learning criterion during the Acquisition 1, Reversal and Acquisition 2 phases for four breeds of sheep (Bluefaced Leicester, Texel, Suffolk and Beulah). Data are mean ± SEM. Pairwise comparisons are between breeds across all four sessions; * $p<0.05$, ** $p<0.01$, $p<0.001$.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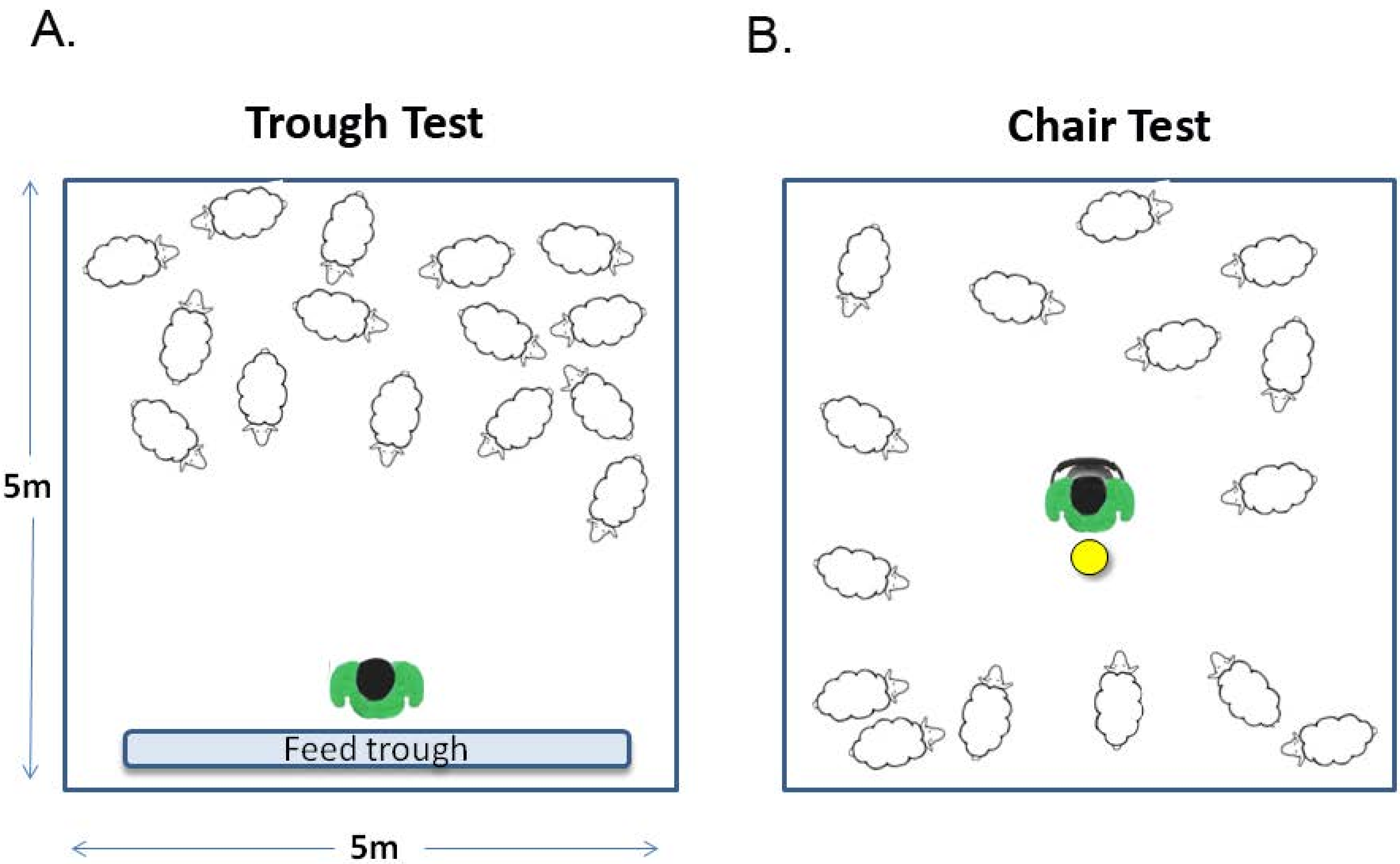
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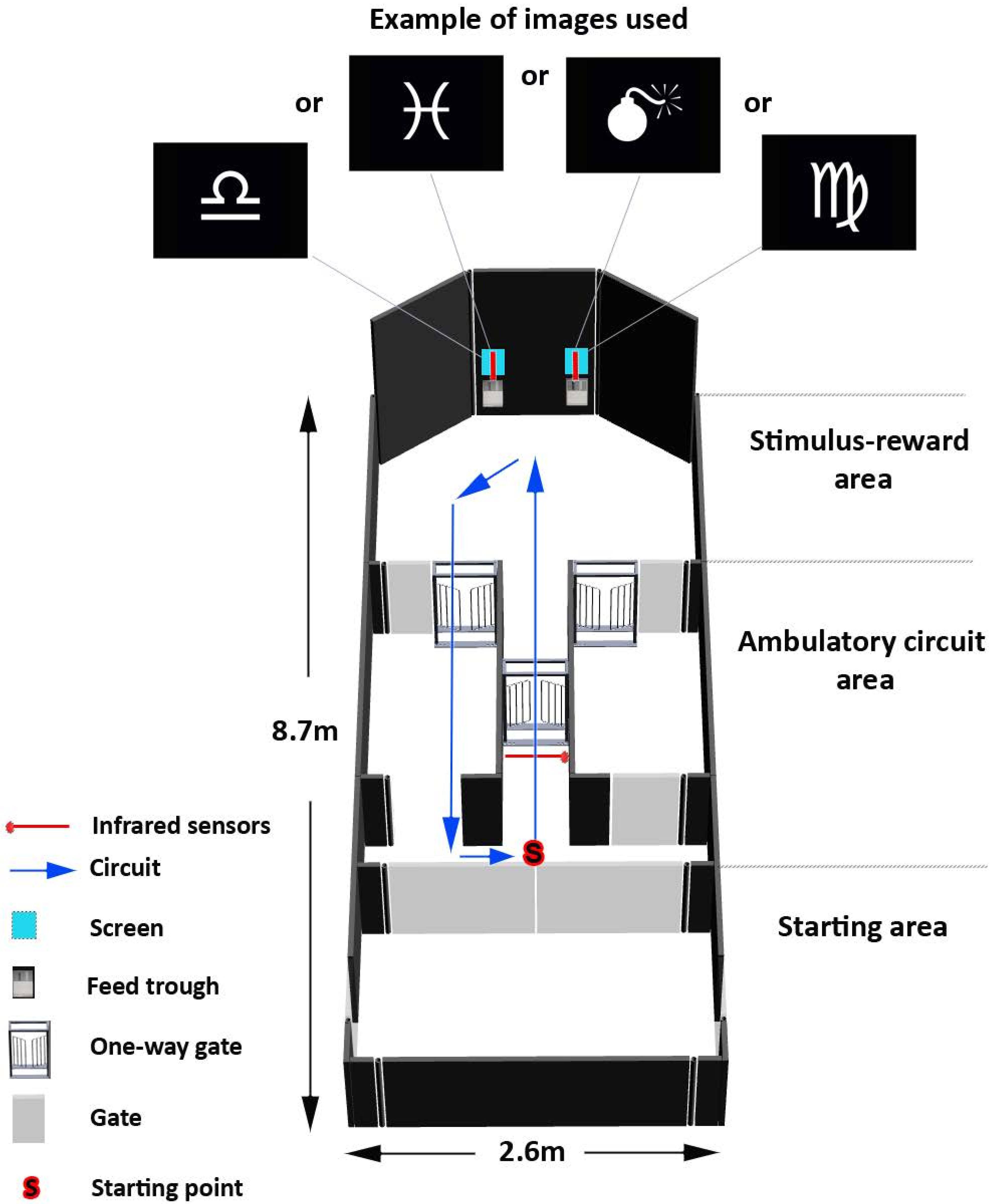
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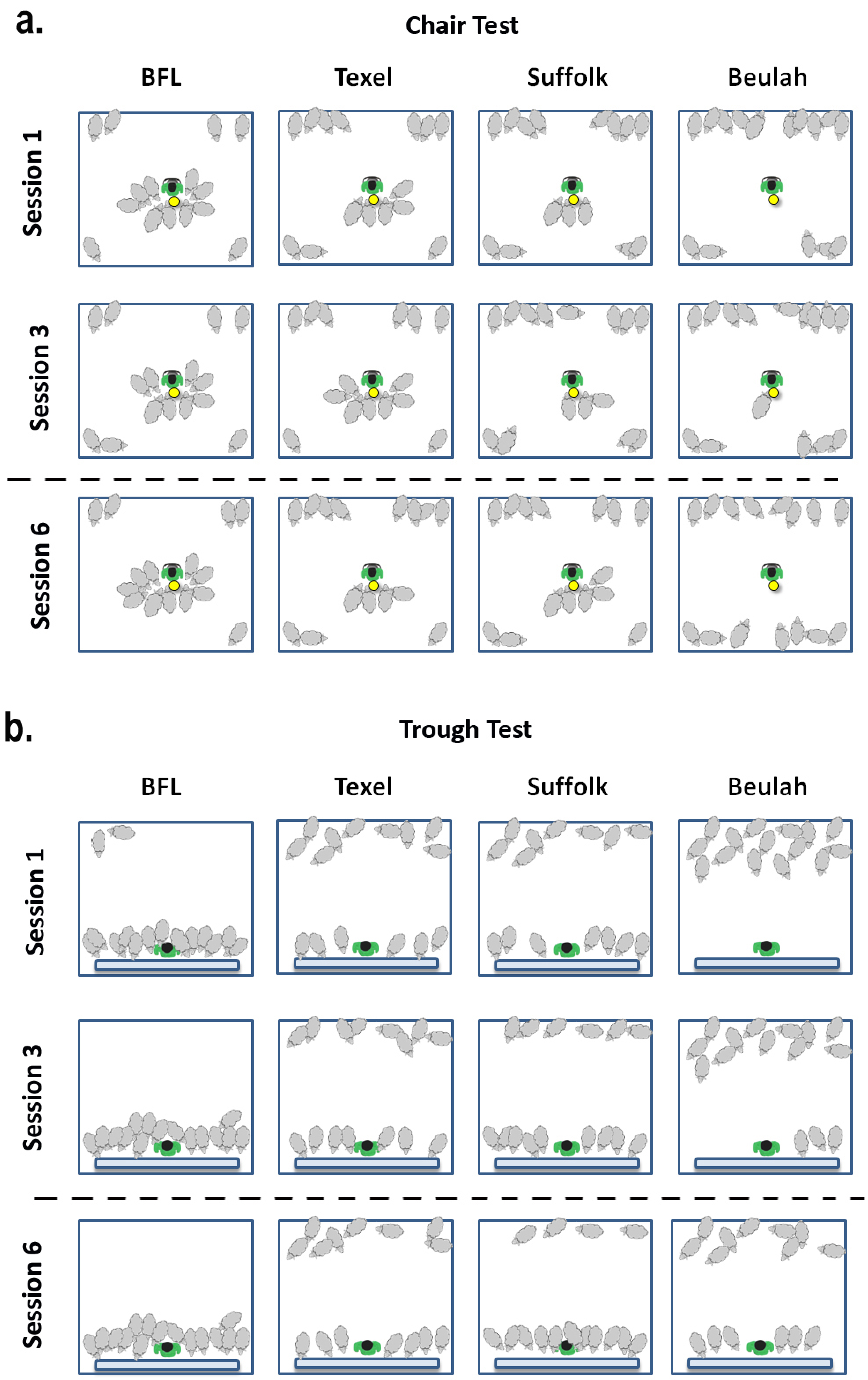

a.
Chair Test
BFL
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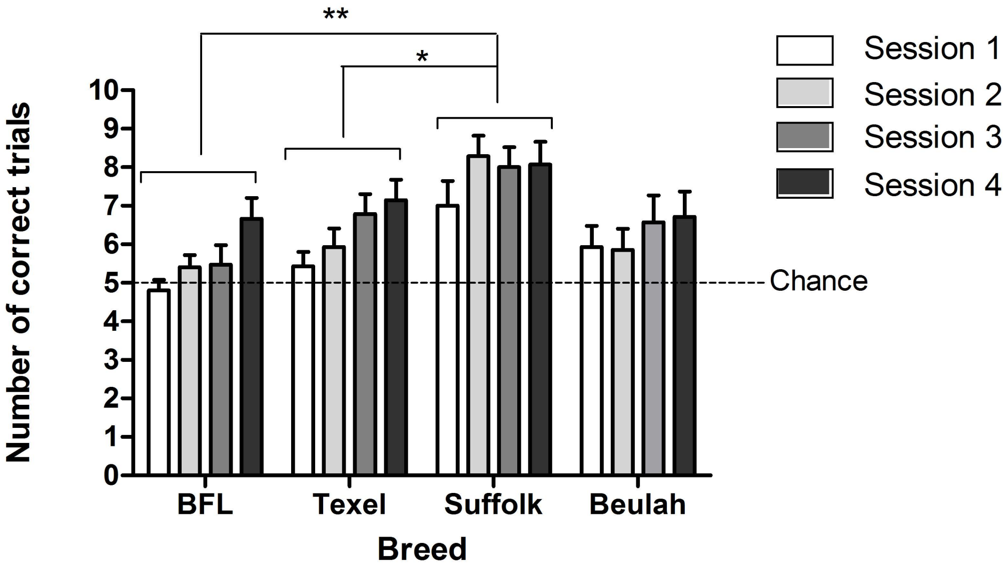
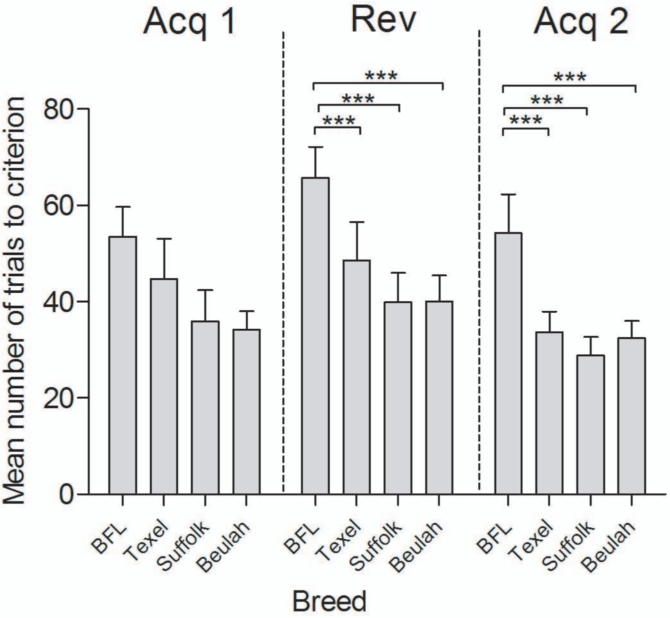
Suffolk
Beulah
Session 1
Session 3
Session 6
b.
Trough Test
BFL
Texel
Suffolk
Beulah
Session 1
Session 3
Session 6



**
*
Session 1
Session 2
Session 3
Session 4
Number of correct trials
10
9
8
7
6
5
4
3
2
1
0
Chance
BFL
Texel
Suffolk
Beulah
Breed



Acq 1
Rev
Acq 2
***
***
***
***
***
***
80
60
40
20
0
Mean number of trials to criterion
BFL
Texel
Suffolk
Beulah
BFL
Texel
Suffolk
Beulah
BFL
Texel
Suffolk
Beulah
Breed