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Response-Inhibition During Problem Solving in Sheep (*Ovis Aries*)

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Response inhibition is a behavioral skill that is important for flexible behavior and appropriate decision making. It requires the suppression of a prepotent but inappropriate action in order to achieve a more advantageous outcome. Response inhibition has been tested in many animal species using the cylinder task. This task requires the self-driven inhibition of an impulse to obtain a visible food reward via a detour rather than a direct but blocked route. We have shown previously using the stop-signal task that sheep can successfully interrupt an already-started response if a reward is going to be restricted. However, it is not known if sheep can show self-driven response inhibition in a task that provides a reward independent of performance. Here, we tested two groups of sheep on the cylinder task (11 Lleyn sheep aged 8 months; 8 Welsh mountain sheep aged ~8 years old). Sheep were trained using an opaque cylinder, and all sheep successfully learned the task. When response inhibition was tested using the transparent cylinder, all sheep performed significantly better than chance, but the older sheep showed a reduced number of correct responses compared to the young sheep ($72.5 \pm 5.0\%$ and $86.4 \pm 4.3\%$ respectively). The results show that sheep have a mechanism for self-regulating their actions in order to retrieve food faster.

Keywords: animal cognition, impulsivity, memory, uglates, learning

Response inhibition is the ability to suppress an intuitive or learned response in place of an alternative action that is more appropriate in the current situation and will result in a better overall outcome (Aron et al., 2007). Self-control is an indicator of higher-order cognitive abilities (Hare, Camerer, & Rangel, 2009). It is important for decision making and has been extensively tested in humans (Hagger, Wood, Stiff & Nikos, 2009; Mischel, Shoda, & Rodriguez, 1989). Better self-control in primates is associated with increased dietary breadth (MacLean, et al., 2014) and more complicated social dynamics, regardless of other abilities (Amici, Aureli, & Call, 2008). In birds, better inhibitory control is associated with larger song repertoire sizes of song sparrows and, hence, with memory and learning (Boogert, Anderson, Peters, Searcy, & Nowicki, 2011). Self-control has only been tested once before in sheep (Knolle, McBride, Stewart, Goncalves, & Morton, 2017). A recent study in goats showed that domesticated goats show some degree of response inhibition, but performance is highly dependent on individual differences (Langbein, 2018).

In a meta-analysis, MacLean et al.(2014) compared the ability of a wide variety of species to apply self-control using the cylinder task. In the cylinder task, animals are trained to obtain food from the open ends of an opaque cylinder. The animals are then presented a transparent cylinder with a visible food reward inside. To perform the task correctly, an animal must overcome the attraction of the food reward, visible inside, and apply a detour method (that they had learned during the training sessions on the opaque cylinder) to reach the reward. That is, they need to inhibit the response of approaching the food directly in order to collect the food reward via the open ends of the cylinder.

In order to perform well on the cylinder task, a species must have both adequate motivation and necessary motor capabilities (MacLean et al., 2014). Motivation is necessary to reduce the time for reward

retrieval, as, in this task, the animal can retrieve the reward whether or not it is applying response inhibition. Sheep match these requirements as they exhibit high motivation for food rewards (Knolle, McBride, Stewart, Goncalves, & Morton, 2017), they are flexible enough to collect the reward from the cylinder (Langbein, 2018), and they have well-developed vision (Knolle, Goncalves, & Morton, 2017), so they should be able to see the food through the wall of the cylinder.

We have previously tested sheep using the stop-signal task (Knolle, McBride, Stewart, Goncalves, & Morton, 2017). The stop-signal task is a classic task of response inhibition. It measures the time taken for an already started response (i.e., the selection of a learned symbol) to be inhibited (cancelled) after a cancellation signal is provided. In order to cancel an already started response, response inhibition is required. Both the stop-signal task and the cylinder task measure the ability of an animal to suppress a response. The important difference between the cylinder task and the stop-signal task is that, in the stop-signal task, sheep are only rewarded for the trials in which they correctly cancelled an already-started response. The stop-signal task includes food restriction, a form of punishment, to condition the animals to the different stimuli. The literature shows that even honey bees can be conditioned using punishment (Smith, Abramson, & Tobin, 1991). In contrast to tasks including punishment, in the cylinder task, the sheep can retrieve the food from the inside of the opaque and transparent cylinder regardless of whether or not they inhibit their response. Based on our previous experience, we hypothesized that sheep would be able to inhibit a prepotent response in order to retrieve the reward out of the transparent cylinder.

In addition to assessing the ability of sheep as a species to inhibit responses, our experiments tested the effect of age on response inhibition in sheep. Numerous studies have shown a correlation between age and response inhibition in humans, with inhibitory control increasing throughout childhood (Carver, Livesey & Charles, 2001; Diamond, 1990; Vlamings, Hare, & Call, 2010). Potential age-related effects on response inhibition have also been reported for dogs, in which success on the cylinder task declined with age (Bray, MacLean, & Hare, 2014).

Method

Subjects

A total of 19 animals were used in this study. These animals were separated into two different groups according to age and breed. One was a group of “old” sheep (8 Welsh Mountain females, aged 8 years, 45-70kg); the second, a group of “young” sheep (11 Lleyn females, aged 8 months old, 38-45Kg). Both groups were permanently held in separate flocks at the University of Cambridge. All sheep lived outdoors with free access to grazing, water, and shelter. The sheep received a food supplement of up to 200 g cereal-based pellets per day (Badminton Country Sheep Nuts, Badminton Country Feeds, UK). These pellets were used as the reward substrate while performing the task. All sheep had previously been used for complex behavioral testing and were familiar with the automated operant apparatus (Knolle, McBride et al., 2017; McBride, Perentos, & Morton, 2016), in which the cylinder task was conducted. The Welsh mountain sheep were tested on an intra-extra dimensional set-shifting task (Morton & Avanzo, 2011), the stop-signal task (Knolle, McBride et al., 2017), and the face-recognition task (Knolle, Goncalves, & Morton 2017). The Lleyn sheep were tested on the intra-extra dimensional set-shifting task (Knolle & Morton, manuscript in process), and the stop-signal task (Goncalves & Morton, unpublished manuscript, that from a preliminary analysis confirms previous results). The current study was carried out in accordance with the UK Animals (Scientific Procedures) Act, 1986; no regulated procedures were carried out during the course of this study.

Apparatus

The apparatus consisted of one of two possible cylinders, both 35 cm in length and 28 cm in diameter and open on both sides (Figure 1). Each cylinder was fixed to a wooden base covered with a black rubber matt (1.5 m × 1.5 m) that was large enough for the sheep to stand on regardless of the angle from which it approached the cylinder. In training sessions, the cylinder used was opaque (Figure 1A); in the probe and memory test, it was transparent (Figure 1B).

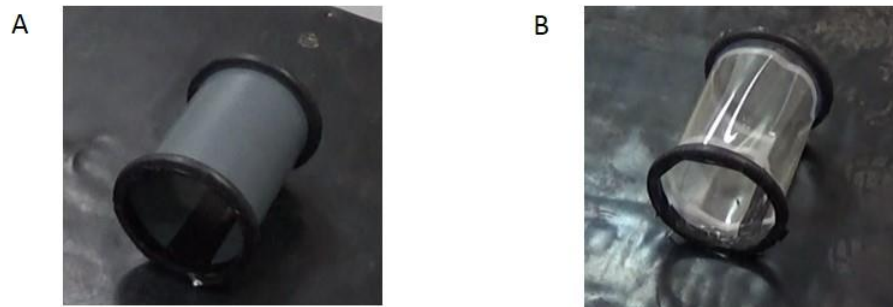


Figure 1. Images of the cylinders used in the experiment. The opaque cylinder (A) was used in training sessions; the transparent cylinder (B) was used in the probe test. Both cylinders had the same dimensions (35 cm in length and 28 cm in diameter) and were open at both ends. Cylinders were fix with screws to a wooden base (1.5 m × 1.5 m) that was covered with a black rubber mat sheet.

Habituation

Sheep are neophobic, so prior to training with the cylinder they were familiarized with the apparatus in the testing area. All animals followed the same habituation protocol: First, animals were brought into the testing area in pairs for 3 to 5 min. Food pellets were scattered on top of a wooden board covered with a black rubber matt identical to the ones onto which the cylinders were attached but without a cylinder. Animals were required to feed from the board. Experimenters did not hand-feed any of the animals inside the testing area. After a maximum of two sessions, all animals were comfortable stepping onto the board and feeding from the board. Second, the animals were introduced to the presence of an external opaque object with closed ends of the same diameter and length as the cylinders that would be used for the training and experimental sessions. The opaque closed cylinder was placed in the middle of the board, and the sheep were again brought into the testing area in pairs for 3 to 5 min. All sheep received one session of habituation to the novel object. During the habituation period, sheep were allowed to explore the testing area and eat any pellets they found on the floor around the board. There was no difference in behavior during the habituation between the two cohorts.

Experimental Protocol for Training, Probe, and Memory Test

This study comprised one stage of training (up to 7 sessions of 10 trials), one probe test, and a memory test that was performed seven weeks after completion of the probe test. All experiments were carried out in the testing area of a semiautomated operant apparatus that allowed the sheep to self-initiate each trial within a session (McBride et al., 2016; Figure 2). All sheep used for this study had been previously trained in other experiments using the testing area of the operant system (Knolle, McBride et al., 2017; Knolle, Goncalves, & Morton, 2017); therefore, no acclimation to the testing area was necessary. Two experimenters were necessary to conduct the study. The experimenters were dressed the same, had the same height and age, were both female, and had similar hairstyles. In order to reduce error rate, Experimenter 1 always dealt with the sheep and Experimenter 2 recorded scores and timing. The second experimenter double-checked timings from the video recordings.

Training consisted of one training session of 10 trials per day. Training sessions were conducted at a pace determined by the sheep and typically lasted 10-15 min. All sessions were video recorded. At the beginning of each session, the sheep were brought as a group into a holding pen where they had free access to water. Sheep were tested individually in no particular order. In each trial, they progressed through the central corridor to the testing area where the wood board with the cylinder was placed (Figure 2). As soon as the animal entered the central corridor, Experimenter 1, who had been standing behind the cylinder, squatted down and showed the reward in an outstretched hand while calling the sheep's name or whistling to get its attention. Experimenter 1 then placed the reward inside the cylinder at the central point and stood up. In the meantime, Experimenter 2 recorded the behavior of the sheep and measured the reaction time using a stopwatch. The time was recorded from when the nose of the sheep passed the one-way gate placed at the central corridor of the operant system until the animal either retrieved the reward (Figure 3A) or touched the exterior of the cylinder (Figure 3B). The side from which Experimenter 1 placed the reward inside the cylinder was counterbalanced across trials. For each trial, the choice behavior was recorded as follows: A correct choice occurred when sheep retrieved the reward directly via the open end of the cylinder without prior touching or exploring the exterior of the cylinder with its hoofs or snout (Figure 3A and Video 1 and 2); an incorrect choice occurred when the sheep touched the exterior of the cylinder with its snout or hoof before retrieving the reward

(Figure 3B and Video 3 and 4) or failed to retrieve the reward (Video 5). After each session, the sheep progressed back into the holding pen. After all sheep had completed their session, they were returned to their home field.

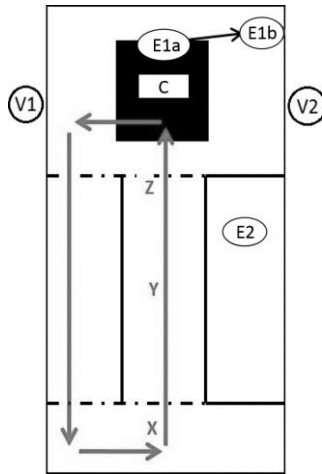


Figure 2. Schematic diagram of the mobile operant system showing the layout used during the training and probe test. The grey arrows show the pathway taken by the sheep. Solid black lines indicate walls. Dashed black lines indicate one-way gates. C stands for cylinder. E1a is the position of Experimenter 1 when placing food inside of cylinder. E1b is the position of Experimenter 1 when sheep are performing task and attempting to obtain the food from the cylinder. E2 is the position of Experimenter 2, who records results and response latencies. V1 and V2 are the positions of video cameras used for recording all training and probe tests. X is the position of the sheep when they are shown food being placed in the cylinder. Y is the position of the sheep as Experimenter 1 begins to move away from the cylinder. Z is the position of sheep (tip of nose) when the stopwatch is started to time the response latency.

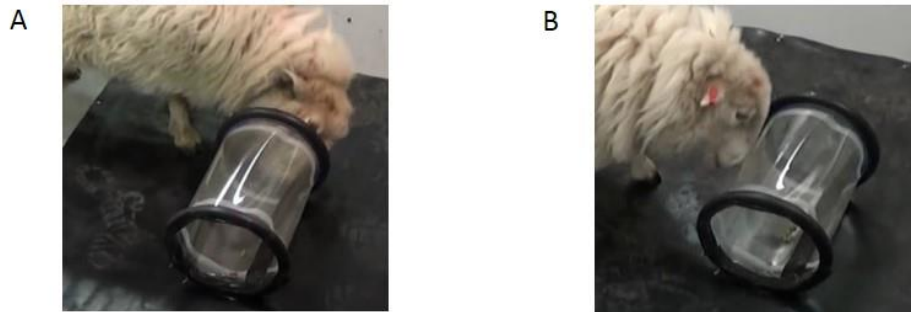


Figure 3. Choice behavior during a probe test. A correct choice (A) was scored when the sheep retrieved the reward directly via the open end of the cylinder without first touching or exploring of the exterior of the cylinder with either hoof or muzzle. An incorrect choice (B) was scored when the sheep touched the exterior of the cylinder with its muzzle or hoof before retrieving the reward.

Training and probe testing differed only in the fact that the apparatus was opaque in training trials and transparent in the probe test. A sheep was moved to the probe test if it succeeded in making a correct first choice in six consecutive trials in one session, or if it had reached an average of 80% correct choices over three consecutive sessions.

Memory testing took place for 7 old and 11 young sheep seven weeks after completion of the probe test. The procedure was identical to that for the probe session using the transparent cylinder. One sheep in the older group was excluded from this part of the study, as she was unwilling to enter the testing arena.

Data Analysis

During all sessions, we measured latencies to food retrieval and correct and incorrect responses. A response was recorded as correct when the animal retrieved the reward without touching or exploring the cylinder prior to the food retrieval. All sheep completed the training and the probe test, all sheep except one from the old cohort completed the memory test. All sheep completed between four and seven training sessions before reaching the learning criterion. For all sheep, we analyzed the first and the final training sessions and the probe and memory test sessions.

Statistics

All statistical analyses were generated using SPSS (Released 2007. SPSS for Windows, Version 16.0. Chicago, SPSS Inc.) or GraphPad PRISM 5.04 (GraphPad Software, Inc., CA 92037 USA). All data are presented as mean \pm SEM. We used parametric statistics, as all assumptions of normality and distribution were met. We applied one-way or repeated measure analysis of variance (ANOVA) with Bonferroni post-hoc tests or Pearson correlations as appropriate. The threshold for statistical significance was set at $p < 0.05$.

Results

In summary, the results reveal a significant improvement for number of correct responses and reduction of latency during training for both groups. Both groups performed above chance in the probe test and the memory test. Furthermore, we found a significant correlation between faster latency and better performance during the probe test and the memory test across all sheep. Three videos illustrate the performance of the sheep. Video 1 shows two training sequences. In the first, the sheep explores the opaque cylinder; in the second, the sheep shows response inhibition to retrieve the food reward. Video 2 shows two sequences during the probe test. In the first sequence, the sheep tries to retrieve the reward directly through the transparent cylinder, showing no response inhibition. In the second sequence, the sheep retrieves the reward via the detour through the opening inhibiting the initial response. Video 3 is another illustration of very good response inhibition behavior, showing a clear interruption of the first direct approach and a successful detour through the opening of the transparent cylinder.

We conducted a repeated measures ANOVA, comparing the number of correct responses (shown throughout as the percentage of total) during training, probe test, and memory test across groups (Figure 4). We found a significant main effect for session, $F(3, 51) = 14.18$, $p < 0.01$, but no significant group effect, $p = 0.12$, or interaction, $p = 0.47$. The Bonferroni corrected post-hoc tests showed a significant increase, $p < 0.01$, in number of correct responses from the first ($56.76 \pm 5.41\%$) to the final training session ($93.64 \pm 2.12\%$) across both groups (Table 1). In the probe test, the number of correct responses dropped significantly, $p = 0.01$, to $79.43\% \pm 3.28$, which was driven by the older group, $p = 0.01$. This was still significantly above chance level, $t(18) = 22.58$, $p < 0.01$. This high number of correct responses did not drop significantly, $p = 1.00$, during the memory test ($72.60 \pm 3.68\%$), showing that the sheep remembered the task.

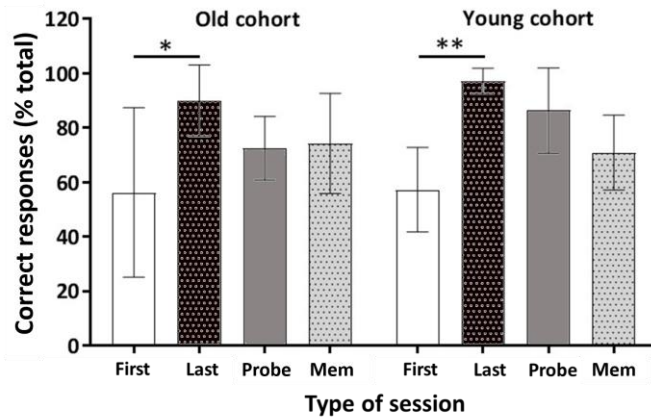


Figure 4. Comparison of correct responses for sheep across training and test sessions. Data are shown as mean \pm SEM of performance in the first (*First*, open bars) and last (*Last*, black bars) training sessions, the probe test (*Probe*, grey bars,) and the memory test (*Mem*, grey/stippled bars). * $p < 0.05$. ** $p < 0.01$.

In an overall repeated measure ANOVA comparing latencies during training, the probe test, the memory test, and across groups (Figure 5), we found a significant main effect for session, $F(3, 51) = 14.28$, $p < 0.01$, but no significant group effect, $p = 0.21$, or interaction, $p = 0.83$. The Bonferroni corrected post-hoc tests showed a significant, $p < 0.01$, latency decrease from the first ($6.32 \text{ s} \pm 0.50$) to the final training session ($3.45 \text{ s} \pm 0.16$) across both groups (Table 1). During the probe test, the latency dropped significantly, $p = 0.03$, to $4.22 \text{ s} \pm 0.28$, which was very similar, $p = 1.00$, to the latency during the memory test, $4.35 \text{ s} \pm 0.40$.

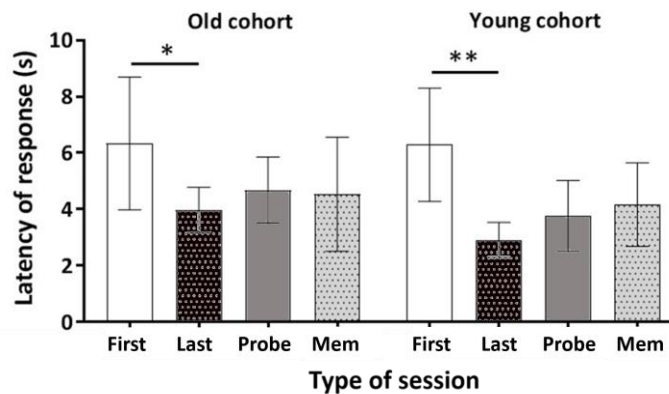


Figure 5. Response latencies for both groups of sheep across training and test sessions. Data are shown as mean \pm SEM of response latencies from the first (*First*, open bars) and last (*Last*, black bars) training sessions, the probe test (*Probe*, grey bars) and the memory test (*Mem*, grey stippled bars). * $p < 0.05$. ** $p < 0.01$

Table 1

Percentage of Correct Responses and Latencies for Each Sheep Individually Across All Analysed Sessions

Sheep number	Training sessions	Correct Responses (% total)				Response Latency (s)			
		First Training	Final Training	Probe Test	Memory Test	First Training	Final Training	Probe Test	Memory Test
Old 1	7	40	70	80	80	7.32	4.02	3.58	3.94
Old 2	5	40	100	70	74.3	5.9	3.52	5.58	4.53
Old 3	5	30	100	60	80	11.49	5.6	6.51	3.59
Old 4	4	100	70	60	70	3.68	3.76	3.96	3.48
Old 5	5	30	90	80	100	6.47	3.85	3.47	3.22
Old 6	4	90	100	90	40	5.9	2.98	3.86	9.15
Old 7	6	90	100	80	60	4.67	3.5	5.93	5.4
Old 8	6	30	90	60	90	5.28	4.58	4.56	2.93
Young 1	4	80	100	60	50	6.61	2.98	5.61	4.05
Young 2	6	50	90	70	70	6.68	3.47	4.78	5.93
Young 3	5	30	100	90	70	5.2	2.89	3.66	3.97
Young 4	5	50	90	100	50	7.49	2.61	2.38	4.12
Young 5	6	50	100	100	80	5.54	2.14	2.17	3.3
Young 6	5	60	100	70	60	10.11	3.69	5.43	5.57
Young 7	4	80	100	70	90	3.41	3.14	4.45	3.01
Young 8	5	60	100	100	80	5.32	3.67	4.5	7.16
Young 9	6	60	100	100	90	3.77	2.68	2.46	2.64
Young 10	5	70	100	90	70	6.16	1.7	3.33	2.4
Young 11	7	40	90	100	70	8.93	3.1	2.62	3.64

We found a significant correlation between faster latency and better performance during the probe test ($r = -0.75$, $p < 0.01$) and the memory test ($r = -0.58$, $p = 0.01$) across all sheep (Figure 6).

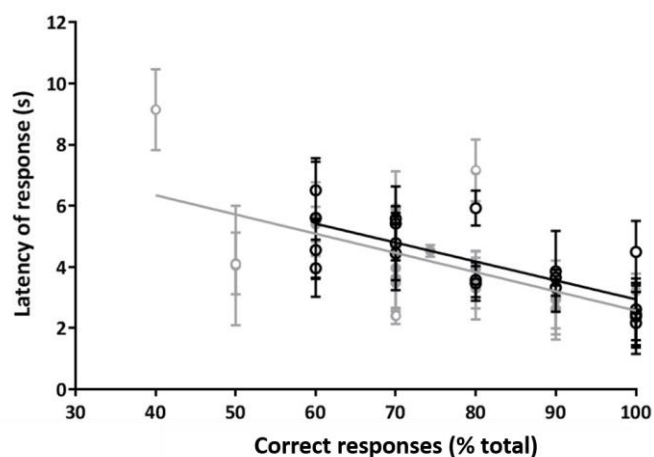


Figure 6. Correlation between latency and number of correct responses during the probe and memory tests. Data show the mean response latency (\pm SEM) of all sheep ($n=19$) plotted against the number of correct responses expressed as a percentage of total responses. During both the probe test (black open symbols, black line) and the memory test (grey open symbols, grey line), the correlation was significant.

Video 1: Training using the opaque cylinder. The sheep walks inside the corridor of the operant system, facing Experimenter 1. Experimenter 1 calls the sheep, shows the sheep the reward that is in her hand, and places the reward inside the opaque cylinder. Then, Experimenter 1 moves away from the cylinder. On the first sequence, the sheep approaches the cylinder directly and explores it with its snout before retrieving the reward from inside the cylinder. On the second sequence, the sheep successfully retrieves the reward from inside the cylinder without prior touching the cylinder with its hoof or snout.

Video 2: Probe test using the transparent cylinder. The sheep walks inside the corridor of the operant system, facing Experimenter 1. Experimenter 1 calls the sheep, shows the sheep the reward that is in her hand and places the reward inside the opaque cylinder. Experimenter 1 then moves away from the cylinder. On the first sequence, the sheep sees the reward through the transparent cylinder and tries to access it directly. The sheep does not show any response inhibition. After exploring the cylinder with its snout, it finally retrieves the reward from inside the cylinder. On the second sequence, the sheep sees the reward through the transparent cylinder but overcomes the visual stimulus and retrieves the reward through the open end of the cylinder without touching the cylinder prior to the attempt.

Video 3: Very good response inhibition in the Probe Test. The sheep walks inside the corridor of the operant system, facing Experimenter 1. Experimenter 1 calls the sheep, shows the sheep the reward that is in her hand, and places the reward inside the opaque cylinder. Then, Experimenter 1 moves away from the cylinder. The sheep stops just in front of cylinder without touching it, showing high levels of self-control, and then the sheep successfully retrieves the reward from inside the cylinder by applying a detour route around the cylinder.

Discussion

Both young and old sheep significantly improved in the task throughout training. Furthermore, both groups performed significantly above chance on the probe test, thus showing that sheep have the ability to self-regulate their behavior by suppressing an inappropriate action. These results extend both our previous findings using a different response inhibition task (i.e., the stop-signal task; Knolle, McBride et al., 2017) and those of a recent study by Langbein (2018), which showed high intra- and interindividual differences in goats performing the cylinder task. Although the younger sheep performed better than the older sheep in the probe test, therefore demonstrating better response inhibition, they showed a slight drop in the number of correct responses in the memory test compared to the older sheep (not significant). All sheep were able to remember the task for at least 7 weeks. This is consistent with other studies that indicate robust memory capacity of sheep (Knolle, McBride et al., 2017; Morton & Avanzo, 2011).

In the probe test, the older group showed a significant decrease in the number of correct responses. This could be due to the novelty of the transparent cylinder. The older group of sheep, although experienced and trained in a variety of tasks, was generally more wary of novelty or changes to their routine. (We do not know the reason for this; it may be because the older sheep were farm sheep obtained for experimental use when they were adults (~1 year), whereas the younger group were obtained specifically for cognitive studies and were first trained as lambs.) Although this was not observed in the younger group of sheep, the group differences did not reach statistical significance. Therefore, while the subtle differences in the number of correct responses between the two groups could suggest that the younger group possessed better response inhibition, it may also have been due to a breed difference (the young sheep were Lleyn, while the older sheep were Welsh Mountain). Behavioral testing shows sheep breed differences in the number of correct responses, with Welsh Mountain sheep outperforming other breeds (McBride, Perentos, & Morton, 2015). Lleyn sheep

were not included in that study, so their relative abilities as a breed are unknown. Both groups lived in similar conditions, and both had experienced experimental testing previously, although their exact experiences did differ. Nonetheless, our results show clearly that both young and old sheep are capable of inhibiting an inadequate response.

The lack of a clear significant difference between the number of correct responses of sheep of different ages is contrary to what we expected from the human literature, which shows that response inhibition increases throughout childhood (Carver, Livesey & Charles, 2001; Diamond, 1990; Vlamings et al., 2010; Zelazo et al., 2003). Little is known about the timescale of functional cognitive and behavioral maturity in sheep, but our results suggest that response inhibition is already matured to an adult level by one year of age. To understand more about ovine brain function maturation, it would be of interest to repeat the cylinder task using sheep younger than one year to determine the age at which inhibitory control matures, as well as sheep between the ages of one and seven to see if response inhibition declines at all with age, as it has been shown in dogs (Bray et al., 2014).

We found a significant positive correlation between speed latency and percentage of correct responses in both the probe and the memory test. This is in contrast to what we found in the stop-signal task (Knolle McBride et al., 2017), in which the number of correct responses increased with increases in response latency (i.e., better performance was related to a slower response). The reason for the difference here might be the fact that, in the cylinder task, sheep are rewarded independently of correct response, whereas the stop-signal task only rewards correct response. Data from the current task extend our previous findings and indicate that sheep can exert self-control over an innate response, which allows them to retrieve a food reward faster. This is an advantageous skill for an animal living in a social group.

Social grouping and experiences influence the ability of an animal to demonstrate inhibitory control in a variety of species. In canine species, differences in inhibitory control are seen between domesticated dogs and wolves (Marshall-Pescini, Virányi, & Range, 2015) and between dogs brought up as pets or in animal shelters (Fagnani, Barrera, Carballo, & Bentosela, 2016). In primates, complex or dynamic social environments are associated with improved inhibitory control (Amici et al., 2008). Sheep are very social animals, with particularly strong abilities for facial recognition and memory (Kendrick, Atkins, Hinton, Heavens, & Keverne, 1996; Knolle, McBride et al., 2017), which may explain their high performance on response inhibition tasks.

The MacLean study showed conflicting results between different tasks aimed to test response inhibition, such as the cylinder task and the A-not-B task (MacLean et al., 2014). In particular, correlations are not always seen between performance in these two tasks (Bray et al., 2014), and performance in each task is influenced differently by particular contextual factors. This may be due in part to the fact that these response inhibition tasks involve aspects of problem solving and understanding of the solidarity principle (Bray et al., 2014). Alternatively, if the tasks are easy for the animal, a ceiling effect may be seen. While such considerations do not decrease the suitability of the cylinder task for use in behavioral and functional testing of sheep, they show that care must be taken in interpreting the results because performance in the task may not correlate directly to the animal's ability to perform inhibitory control. This task would be even more powerful if used in parallel with other inhibitory control tasks, such as the stop-signal task (Knolle, Goncalves et al., 2017). These studies show that sheep can learn to inhibit an already-initiated response efficiently, regardless of whether the behavior is shaped by withholding a reward/punishment. The cylinder task extends the repertoire of behavioral tasks that can be used to study sheep behavior and is particularly interesting, as it does not require any form of punishment. Sheep are increasingly being used as animal models of human diseases (Morton & Howland, 2013 Pouladi, Morton, & Hayden, 2013). Many neurological diseases, including Huntington's disease (HD), have impulse control deficits (Novak & Tabrizi, 2010). Because there is a

transgenic sheep model of HD (Jacobsen et al., 2010; Skene et al., 2017), this task would be particularly useful for studying impulse control in the HD sheep.

In conclusion, our findings show that sheep are able to successfully inhibit response triggered by a visual stimulus. Furthermore, sheep are able to remember this task correctly for at least 7 weeks. Together our results support the use of the cylinder task to measure response inhibition as an element of self-control and self-regulation and suggest that it can be included in a battery to test ovine executive function.

Acknowledgements

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