Journal of Veterinary Behavior 33 (2019) 1–6

Contents lists available at ScienceDirect

Journal of Veterinary Behavior

journal homepage: www.journalvetbehavior.com

Canine Research

Does the cognitive bias test in dogs depend on spatial learning?

Margaret E. Gruen [a], Melanie L. Foster [a], Lucia Lazarowski [b,1], Amanda Jeffries [b,2], Barbara L. Sherman [a], David C. Dorman [b,*]

[a] Department of Clinical Sciences, North Carolina State University, College of Veterinary Medicine, Raleigh, North Carolina
[b] Department of Molecular & Biomedical Sciences, North Carolina State University, College of Veterinary Medicine, Raleigh, North Carolina

ARTICLE INFO

Article history:
Received 11 October 2018
Received in revised form
6 April 2019
Accepted 11 April 2019
Available online 18 April 2019

Keywords:
canine
cognition
delayed non-matching to position

ABSTRACT

Cognitive bias tests have been used to measure affective states in dogs. The results may also involve spatial learning and memory when location is used as the cue. In this study, we evaluated the performance of 16 Labrador retriever dogs with a cognitive bias test that used spatial location as the cue and compared the results to the dogs' performance on a delayed nonmatching to position (DNMP) operant procedure. All dogs completed the cognitive bias test, whereas only 9 of 16 completed DNMP acquisition criteria within a maximum of 300 trials (mean ± SEM for successful dogs = 187.8 ± 19.2 trials). A negative correlation was observed between the number of trials required for DNMP acquisition and the mean latencies to the near positive ($P = 0.001$, $r^2 = 0.56$, $n = 16$) and near negative ($P = 0.013$, $r^2 = 0.39$, $n = 16$) ambiguous locations on the cognitive bias test. For the 9 dogs who met DNMP acquisition criteria within 300 trials, this correlation remained, with a significant negative correlation observed for the near positive ($P = 0.01$, $r^2 = 0.64$) and near negative ($P = 0.055$, $r^2 = 0.43$) ambiguous positions and the number of DNMP trials. The observed association between a classic test of spatial working memory (DNMP) and the cognitive bias test suggest that the cognitive bias test may also rely on spatial learning in some dogs. This finding suggests that the effect of spatial learning ability may need to be acknowledged in tests that use location as the discriminatory cue.

Introduction

Cognitive bias tests have been used to assess affective state in several species including—among others—humans, rodents, and dogs. Over the course of a cognitive bias test session, animals are trained to associate one cue with a reward and another cue with a lesser or absence of reward, followed by testing trials with intermediate, ambiguous cues (Mendl et al., 2009). In some versions of the cognitive bias test, an aversive stimulus is used as the negative stimulus, thus evaluating how animals assess the likelihood of positive or negative outcomes (Brilot et al., 2009; Burman et al., 2009). There is evidence from humans (Mogg et al., 2006) and rodents (Burman et al., 2009; Harding et al., 2004) that affective state can affect judgments about these ambiguous stimuli, with positive affective states being associated with more optimistic evaluations of ambiguity (Burman et al., 2011).

Cognitive bias tests have also been used to evaluate and improve the welfare of animals (Burman et al., 2011; Mendl et al., 2009) and as a potential measure of therapeutic efficacy for interventions. For example, a "pessimistic" cognitive bias has been found in shelter dogs with separation-related behavior (Mendl et al., 2010), whereas a move toward an "optimistic" cognitive bias has been seen in dogs receiving fluoxetine as a treatment for separation-related distress (Karagiannis et al., 2015). Despite being used to assess affective states, some cognitive bias involving location as the cue may be confounded by individual differences spatial learning and memory (Doyle et al., 2010).

Spatial learning and memory—the ability to learn about locations and orientations of objects in the environment—are critical to an animal's ability to survive and reproduce. Memory for locations of previously visited sites containing food sources, mates, or predators requires sophisticated spatial cognition and memory in which a number of learning strategies may be adapted, including the use of visual landmarks (Fiset, 2007; Macpherson and Roberts, 2010). Spatial learning and memory also play important roles in the

* Address for reprint requests and correspondence: David Dorman, DVM, PhD, DABVT, DABT, NCSU College of Veterinary Medicine, 1060 William Moore Drive, Raleigh, NC 27607. Tel/Fax: +1 (919) 513-6336.
E-mail address: David_dorman@ncsu.edu (D.C. Dorman).
[1] Present address: Auburn University, Auburn, AL.
[2] Present address: Fort Jackson, SC.

https://doi.org/10.1016/j.jveb.2019.04.002
1558-7878/

performance of working dogs used for various types of searches (Fiset et al., 2000).

The delayed nonmatching to position (DNMP) procedure has been used to assess spatial working memory in rodents (Yhnell et al., 2016) and dogs (Chan et al., 2002, Adams et al., 2000; Milgram et al., 1999). The DNMP test involves presenting the subject with one object (the sample), followed by a delay and then the subject chooses between the sample and a second object in a new location (the correct choice).

The objective of this project was to evaluate whether performance of Labrador retrievers on the DNMP and cognitive bias tests were correlated—suggesting that the cognitive bias test may also be dependent on spatial learning in dogs. If the cognitive bias test were associated with spatial learning and memory, it could prove to be a more rapid method for assessing spatial learning.

Materials and methods

Subjects

Male (n = 8) and female (n = 8) Labrador retrievers (1–3 years of age) participated in this study. Dogs were individually housed in temperature- and humidity-controlled indoor kennels (1.5 m × 2.4 m), fed a canine dry ration twice daily (Iams Mini Chunks, P & G Pet Care, Cincinnati, OH), provided water ad libitum, and were provided several forms of enrichment (Sherman et al., 2015). This study was performed in an AAALAC International accredited facility at North Carolina State University (NCSU) College of Veterinary Medicine. All experimental protocols were reviewed and approved by the NCSU Institutional Animal Care and Use Committee and the US Office of Naval Research Animal Care and Use Review Office.

Delayed nonmatching to position (DNMP) test

Apparatus

The testing apparatus was a 66 cm × 178 cm × 91 cm plastic chamber based on the Toronto General Testing Apparatus (TGTA, CanCog Technologies, Toronto, Canada) for dogs as described previously (Lazarowski et al., 2014; Figure 1A). The chamber was divided into two areas by stainless steel bars. The dog remained in one area, and stimuli were delivered to the dog in the other area. The experimenter sat outside the chamber, behind a wall that contained a one-way mirror and a hinged door measuring 20 cm high. The hinged door allowed the experimenter to slide a black, Plexiglas tray with three wells toward the dog. Each well could accommodate the stimulus, a white plastic block. The reward for correct response was an approximately 2 cm piece of Pup-Peroni® original bacon flavor treat (DelMonte Corp., IA) that was placed in the well beneath the correct stimulus. An inaccessible food reward of the same type, amount, and age was attached to the bottom of the S- object to control for odor cues.

The chamber and equipment were wiped with a dry cleaning towel in between subjects. After all subjects completed testing for the day, the chamber was cleaned with neutral table cleaner disinfectant solution (50 mL Virkon powder dissolved in 600 mL of water).

Data were collected using DogCog™ software (CanCog Technologies, Toronto, Canada) on a computer running Windows 7 interface. The software was used to randomize the location of the rewarded well on each trial, signal the start of a trial with a tone, and time response latencies and intertrial intervals. A keystroke recorded the dog's response on each trial.

Test procedures

Before beginning the DNMP phase, all dogs underwent a pretraining protocol to acclimate them to the testing apparatus and to procedures including reward-approach learning, object-approach learning, and an object discrimination and reversal task (Lazarowski et al. 2014). Pretraining was conducted 5 days per week.

For all procedures, a trial began with the sound of a digital tone immediately followed by the presentation of a single object (white block) serving as the sample, located in one of three positions on the tray. Following a 2-second inspection interval, the tray was fully advanced and displacement of the coaster holding the object was rewarded. The tray was then removed, and a 10-s delay was simultaneously initiated. Following the delay, the tray was again presented with two identical white blocks, one in the original sample position and another in one of the other two positions. After a 2-s inspection interval, a second tone sounded, and the tray was fully presented. Responses to the object in the position different than the sample (S+) were rewarded. A correction procedure, used

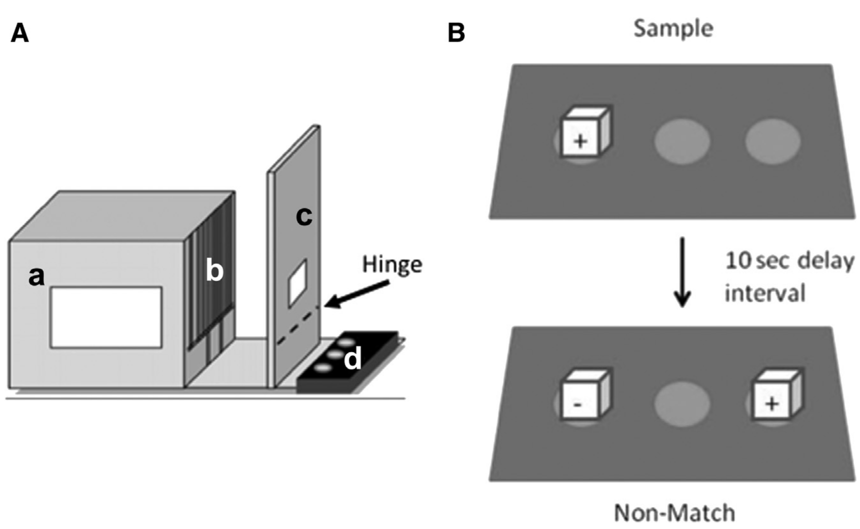

Figure 1. (A). Schematic of the testing apparatus used in cognitive assessment testing (from Araujo and Milgram, 2004). (a) The test box where the dogs entered from a ramp; (b) The front of the test box that consisted of stainless steel bars of adjustable height that provided three openings to access the objects; (c) A plastic screen between the experimenter and animal had a one-way mirror and a hinged door, which was raised to present the sliding tray with objects to the animals; (d) A black Plexiglas presentation tray that had three food wells, two lateral and one medial. (B). Delayed nonmatching to position (DNMP) paradigm. Modified from Adams et al., 2000.

only on the first error of the session, allowed the dog to continue to respond after an incorrect response (S−) until the food reward was obtained. The remainder of the trials in the session ended after the first response, regardless of whether it was correct or incorrect. Each trial was separated by a 30-s intertrial interval. The blocks were wiped in between trials and the blocks were interchanged throughout the session to control for scent marking of the objects. DNMP sessions consisted of 12 trials in a session, with each position (center, left, and right) serving as the S+ an equal number of times. A two-part criterion for successful acquisition was used for this task. First, the dog had to have either 11/12 correct responses or better on one session, 10/12 or better on two consecutive sessions, or a cumulative score over 80% correct on three consecutive sessions. The second part of the criterion required 70% correct or greater over 3 consecutive sessions. Figure 1B provides a schematic representation of the test.

Cognitive bias test

After completion of the DNMP test, the cognitive bias test was conducted using previously published methods (Mendl et al., 2009). The test room measured 4.7 m × 7.2 m (Figure 2). The start position and locations where bowls were to be placed were marked with tape. Before the start of each trial, the dog was removed from the room while one investigator placed a large stainless-steel food bowl with or without a small piece of a food reward (Pup-Peroni®) at one of five predetermined locations 4 m in front of the designated starting position. The dog was then led into the room and brought to the start position, where a second investigator (handler) would simultaneously release the collar and give a verbal prompt ("Go") to allow the dog to approach the bowl. The handler remained in the start area and looked down at the floor, not at the test area. If the dog did not leave the start position within three seconds, the prompt was repeated by the handler. If the dog still remained at the start position, another prompt was given by the handler, and no further prompts were provided. The latency to reach the bowl, defined as the time elapsed between the first release and the dog crossing the plane extending up from the bowl, was recorded for each trial using a stopwatch.

During the acclimation phase, dogs were trained that there was one "positive" location where the bowl would contain food, and one "negative" location on the opposite side where no food was provided. For half the dogs, the positive location was on the right side as they faced the test area, and for the other half, it was on the left. Initially, each dog received two consecutive positive trials (bowl placed in the positive location with a food reward in it) followed by two negative trials (bowl placed in the negative location with no food reward). Subsequently, positive and negative training trials were presented in a pseudorandom order, with no more than two trials of the same type being presented consecutively. During the first 10 training trials, if the dog did not approach the bowl within 30 seconds, the test trial was terminated, and the dog was taken to the bowl (regardless of whether a reward was present). All dogs received a minimum of 15 training trials (any trial that terminated at 30 seconds was still considered a valid training trial). To proceed to the testing phase, dogs had to have at least 15 training trials and meet the criteria for a learned association between the positive location and a food reward; dogs had to have a shorter latency to reach the positive location relative to the negative such that their longest latency to the bowl on the 3 preceding positive trials was shorter than the shortest latency to reach the bowl on the 3 most recent negative trials. On each trial, dogs were given a maximum of 30 seconds to visit the bowl. If they had not visited it by this time, the trial was terminated, a time of 30 seconds was recorded, and the next trial was initiated.

Testing began immediately after the learning criterion was achieved. Test (probe) trials were identical to training trials except that the bowl (without a food reward) was placed at one of three ambiguous locations equally spaced 1.4 m apart along an arc 4 m from the dog's start position and between the positive and negative locations (Figure 2). The three locations were near-positive (NP: 1.4 m from the positive and the middle locations), middle (M, halfway along the arc, 2.8 m from the positive and negative locations), and near-negative (NN: 1.4 m from the negative and middle locations). Three probe test trials were presented at each location (nine test trials in total) in the following order: M, NP, NN, NP, NN, M, NN, M, NP (each location was presented first, second, or third in each block of three test trials). The purpose of the test trials was to investigate how dogs responded to these ambiguous locations and whether they tended to run quickly to them (indicating anticipation of a food reward—an "optimistically" biased judgment of the ambiguous cue) or more slowly (indicating lower anticipation of food—a "pessimistically" biased judgment).

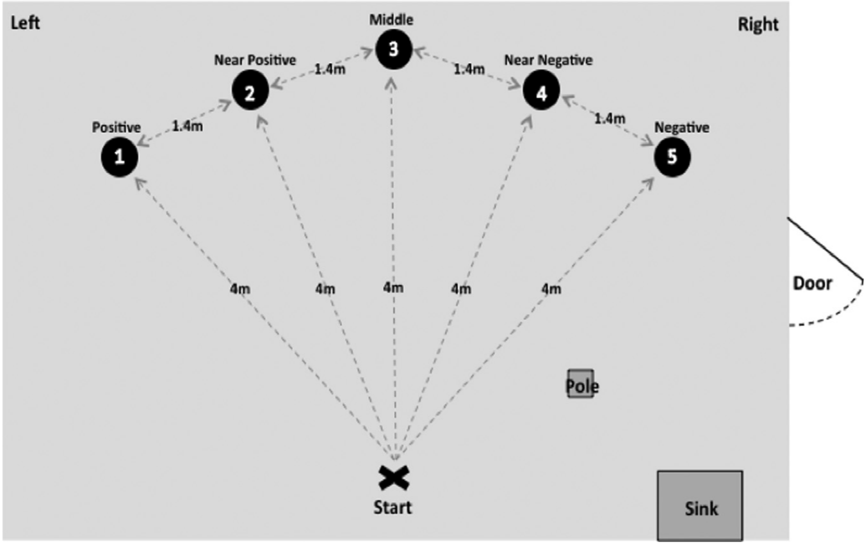

Figure 2. Cognitive bias testing facility layout for a dog trained for the left side bowl to be positive and the right side bowl to be negative. Distance from one bowl position to the next is 1.4 m.

The testing phase began with two consecutive positive trials followed by two consecutive negative trials. Following that, each probe test trial was separated from the next by four pseudorandom training trials (positive and negative locations), identical to those used in the training phase, to maintain and reinforce the associations between the positive and negative locations and reward. After the last ambiguous location test trial, four more training trials were run, and a final trial was then conducted in which an empty bowl was placed in the positive location. The purpose of this odor control trial was to determine if dogs ran just as quickly to an empty bowl in this location as to the usual baited bowl and hence were not relying on odor cues to detect whether the bowl was baited. The entire test phase involved an additional 40 training trials, 9 probe test trials, and one empty bowl trial for a total of 50 additional trials beyond the initial training phase.

Data analysis

Response accuracy has proven to be a powerful behavioral indicator of learning and memory performance in dogs tested in the CanCog™ system (Callahan et al., 2000; Chan et al., 2005; Head et al., 1998; Milgram, 2003; Milgram et al., 1994; Tapp et al., 2003). For the DNMP task, the sum of total number of errors committed during the acquisition phase was used to calculate error scores for error rates (trials in which an error occurred/total number of trials during acquisition phase). An ANOVA was used to determine whether sex was significantly associated with error scores. For some analyses, the number of trials was right censored at 300 with the error rate calculated accordingly.

For the cognitive bias task, mean latencies to reach the bowl during each of the three types of test trial (NP, M, NN) and during training trials (P, N) were calculated for each dog. Comparisons between mean latencies to reach the bowl were performed using a matched-pairs *t*-test. To control for differences in dog size and gait speed, each dog's test trial latency was also adjusted according to its mean "baseline" latencies during training trials (Mendl et al., 2010). The adjusted score is calculated by:

$$\text{Adjusted latency} = 100 \times \left(\frac{\bar{x}\ \text{probe} - \bar{x}\ \text{positive}}{\bar{x}\ \text{negative} - \bar{x}\ \text{positive}}\right)$$

where, $\bar{x}$ is the mean latency for a given position.

This adjusted score expresses all probe test latencies as a percentage of the difference between each dog's baseline mean latencies to the positive and negative locations. Overall adjusted mean values for a parameter were calculated before completing data analysis. Correlations between adjusted latencies and DNMP test were examined using Spearman ρ.

Results

DNMP

All dogs were able to complete pretraining phases in the TGTA apparatus. One female dog did not successfully complete acquisition of the object discrimination and reversal tasks. Because of her low motivation, she was not tested on the DNMP task. Six additional dogs did not meet acquisition criteria for the DNMP task (terminated at 300 trials, 25 days of training). Individual results for the DNMP task are presented in Table. The dogs in our cohort segregated into two DNMP performance categories: (a) successful dogs, who achieved acquisition in <300 trials, and (b) unsuccessful dogs (acquisition did not occur before 300 trials). Among the successful dogs who acquired this task (n = 9), the mean (±SEM) number of trials to acquire the task was 187.8 ± 19.2 trials. The mean (±SEM) error rates in the successful and unsuccessful DNMP learners were 34.9 ± 1.0% and 45.7 ± 2.7%, respectively. Sex did not have a statistically significant effect on the number of trials needed to reach criterion (ANOVA, n = 9, df = 1, *P* = 0.59) or the associated overall error rate (ANOVA, n = 9, df = 1, *P* = 0.36) for dogs that completed the DNMP task.

Table

Number of errors and total trials required to reach criterion on the delayed non-match to position (DNMP) and the cognitive bias tasks. DNMP criterion: First, the dog had to have either 11/12 correct responses or better on one session, 10/12 or better on two consecutive sessions, or a cumulative score over 80% correct on three consecutive sessions. The second part of the criterion required 70% correct or greater over 3 consecutive sessions. Cognitive bias criterion: A minimum of 15 training trials; dogs had to have a shorter latency to reach the positive location such that their longest latency to the bowl on the 3 preceding positive trials was shorter than the shortest latency to reach the bowl on the 3 preceding negative trials

Subjects	Sex	Color	DNMP errors	DNMP total trials	Cognitive bias training trials
Fast DNMP learners					
Ace	M	B	35	108	15
Baxter	M	B	60	156	33
Honey	F	Y	47	142	16
Hunter	M	B	43	144	26
Macks	M	B	96	276	24
Mercy	F	B	61	168	43
Ruby	F	Y	87	252	18
Valentine	F	B	96	240	16
Wizard	M	B	70	204	24
Slow DNMP learners					
Annie	F	Y	115	300	16
Bullet	M	Y	137	300	22
Dakota	F	B	122	300	15
Jimmy	F	B	138	300	15
Reno	M	Y	172	300	18
Rip	M	B	139	300	33
Did not attempt DNMP					
Piper	F	Y	N/A	N/A	17

Cognitive bias

The number of training trials to meet criterion for the cognitive bias test for all dogs varied from 15 to 43 training trials (Table). The mean number (±SEM) of training trials was 21.9 ± 2.1. There was no significant correlation between the number of trials for acquisition of the DNMP task and the number of trials for acquisition of the cognitive bias task (n = 9, Spearman ρ = −0.160, *P* = 0.57). Throughout the test phase, the bowl was placed at both the positive and negative positions a total of 20 times each per dog, at the near positive, middle, and near negative position 3 times each per dog, and at the odor control position (positive position with no reward) 1 time per dog. Mean latencies (±SEM) for each bowl position during the cognitive bias testing phase can be seen in Figure 3. The mean (±SEM) latency to the odor control (bowl placed in the positive position, but with no reward) was 2.14 ± 0.07 sec. This value was significantly lower than the mean (±SEM) time to reach the positive location 2.70 ± 0.17 sec (matched-pairs *t*-test, n = 16, df = 15, t= 3.31, *P* = 0.005), demonstrating that the dogs were not using odor cues to determine whether or not to approach the bowl.

A significant correlation was found between the adjusted mean latencies of the near positive (Spearman ρ = −0.634, *P* = 0.011) and near negative (Spearman ρ = −0.63, *P* = 0.011) ambiguous positions and the number of DNMP trials (all dogs). No significant correlation was found between adjusted mean latency of the middle ambiguous position and the number of DNMP trials (Spearman ρ = −0.437, *P* = 0.103).

A significant correlation remained present when the data from only the subset of dogs (n = 9) who completed the DNMP task were analyzed (Figure 4). In this case, a statistically significant correlation

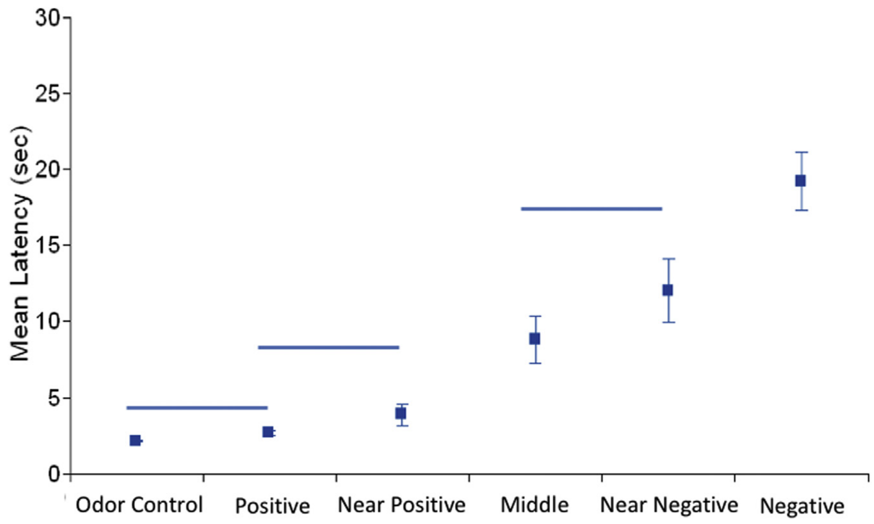

Figure 3. Unadjusted mean (±SEM) latencies observed during the test phase on trials where the bowl was placed at the positive and negative training locations, and at the three test locations: near positive, middle, near negative. Bars shown above the data indicate data pairs that were statistically equivalent (Wilcoxon test). All other data pairs are statistically different from each other.

was seen for the near positive (Spearman $\rho = -0.85$, $P = 0.004$) and near negative (Spearman $\rho = -0.783$, $P = 0.013$) ambiguous positions and the number of DNMP trials. No significant correlation was found between adjusted mean latency of the middle ambiguous position and the number of DNMP trials in dogs that completed the DNMP task (Spearman $\rho = -0.450$, $P = 0.224$).

Discussion

On the DNMP task, dogs segregated into two DNMP performance categories: (a) fast learners, and (b) slow learners (acquisition did not occur before 300 trials). Head, et al. (1995) have reported that a higher proportion of aged dogs could not acquire the DNMP task relative to young dogs, and the acquisition rate was correlated with age. In the present study, all dogs were $\leq$ 3 years old, making age an unlikely contributor to the dogs' ability to acquire the task. Sex of the dog was also not a determinant for performance in our cohort of Labrador retrievers; however, this was a small sample and may be subject to a Type II error (incorrectly failing to reject the null hypothesis of no difference based on sex). There is still much debate over sex differences in spatial working memory in animals (Jonasson, 2005). In rodent working memory tasks involving the retention of largely spatial information, such as the Morris water and the radial-arm maze procedures, males typically outperform females (Jonasson, 2005). There are several published rat studies using the same procedure employed in our dogs that also assessed the behavior of both male and female rats (Aarde and Jentsch, 2006; Marrs et al., 2005). In these studies, female rats performed better than males. However, in other tests of spatial working memory, there are either no differences between the sexes or better performance by females (Aarde and Jentsch, 2006).

This study investigated whether the cognitive bias test may also depend on spatial memory. The results showed an association between performance on a classic assessment of spatial memory, the DNMP, and cognitive bias tests such that dogs who took longer to learn the DNMP also moved more quickly toward the ambiguous locations. These findings suggest that the cognitive bias test includes a spatial learning component and may not be singularly defined by valence or an animal's affect. Several possibilities may explain this association. First, spatial learning may affect performance as dogs learn, over time, that certain bowl positions in the cognitive bias test are unrewarded. Those dogs who learned this more quickly (and thus had longer latencies to the ambiguous locations) were also faster to acquire the DNMP task. This interpretation is in agreement with data collected in sheep which "show a significant decline in the total number of approaches to ambiguous positions over time because the sheep learned that these ambiguous locations were unrewarded" (Doyle et al., 2010). Second, a "pessimistic" or "optimistic" cognitive affect could influence performance and persistence in the DNMP task such that dogs with an optimistic affect could be more motivated to continue testing. However, all dogs continued to participate in DNMP testing despite making errors. Third, an unknown variable may be affecting performance in both tasks, and this requires further evaluation in a larger sample and with other breeds of dogs. One way to test this

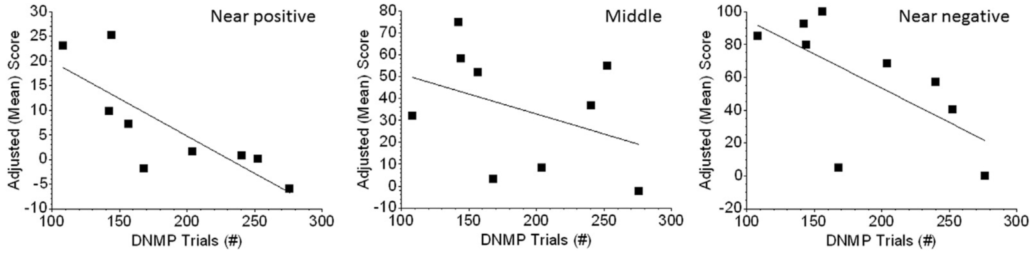

Figure 4. Significant linear correlation ($P < 0.05$) seen between the adjusted mean latencies of the near positive and near negative ambiguous positions and number of DNMP trials needed to reach criterion on this task. Data are also shown for the middle position (not significant).

association would be to use a cue other than location for testing cognitive bias. Recent studies with other species have used color rather than location (calves: Daros et al., 2014; Neave et al., 2013). The spatial learning component of the cognitive bias test in dogs should not be overlooked and warrants further exploration. It is important to note that our study is correlational and can only suggest an association, not causality.

Acknowledgment

This work was funded by a grant to K2 Solutions, Inc. from the United States Office of Naval Research (ONR). Lisa Albuquerque and Michael Hoglund provided logistical support. We thank the NCSU Laboratory Animal Resources staff for excellent animal care. Beth Case, Heather Waterman, Matthew Clark, Alyxandra Reinhardt, and Claire Walker assisted with test implementation. We appreciate the technical guidance provided by Dr. Rachel Casey (Director of Canine Behavior and Research, Dogs Trust/Royal Veterinary College).

Ethical considerations

Experimental protocols were reviewed and approved by the NCSU Institutional Animal Care and Use Committee and the US Army Medical Research and Materiel Command Animal Care and Use Review Office. The NCSU CVM is accredited by AAALAC International.

References

Aarde, S.M., Jentsch, J.D., 2006. Haploinsufficiency of the arginine-vasopressin gene is associated with poor spatial working memory performance in rats. Horm. Behav. 49, 501–508.
Adams, B., Chan, A., Callahan, H., Siwak, C., Tapp, D., Ikeda-Douglas, C., Atkinson, P., Head, E., Cotman, C.W., Milgram, N.W., 2000. Use of a delayed non-matching to position task to model age-dependent cognitive decline in the dog. Behav. Brain Res. 108, 47–56.
Araujo, J.A., Chan, D.F., Winka, L.L., Seymour, P.A., Milgram, N.W., 2004. Dose-specific effects of scopalomine on canine cognition: Impairment of visuospatial memory, but not visuospatial discrimination. Psychopharmacology 175, 92–98.
Brilot, B.O., Normandale, C.L., Parkin, A., Bateson, M., 2009. Can we use starlings' aversion to eyespots as the basis for a novel "cognitive bias" task? Appl. Anim. Behav. Sci. 118, 182–190.
Burman, O., Mcgowan, R., Mendl, M., Norling, Y., Paul, E., Rehn, T., Keeling, L., 2011. Using judgement bias to measure positive affective state in dogs. Appl. Anim. Behav. Sci. 132, 160–168.
Burman, O.H.P., Parker, R.M.A., Paul, E.S., Mendl, M.T., 2009. Anxiety-induced cognitive bias in non-human animals. Physiol. Behav. 98, 345–350.
Callahan, H., Ikeda-Douglas, C., Head, E., Cotman, C.W., Milgram, N.W., 2000. Development of a protocol for studying object recognition memory in the dog. Prog. Neuropsychopharmacol. Biol. Psychiatry 24, 693–707.
Chan, A.D.F., Nippak, P.M.D., Ikeda-Douglas, C.J., Head, E., Cotman, C.W., Murphey, H., Muggenburg, B., Milgram, N.W., 2002. Visuospatial impairments in aged canines (Canis familiaris): The role of cognitive-behavioral flexibility. Behav. Neurosci. 116, 443–454.
Chan, J.W.C., Araujo, J.A., Zicker, S.C., Pun, T.W.C., Milgram, N.W., 2005. Effect of feeding patterns on performance of a visuospatial memory task in the beagle dog: A novel cognitive-based protocol for assessing satiety. Prog. Neuropsychopharmacol. Biol. Psychiatry 29, 481–488.
Daros, R.R., Costa, J.H.C., von Keyserlingk, M.A.G., Hotzel, M.J., Weary, D.M., 2014. Separation from the dam causes negative judgement bias in calves. PLoS One 9, e98429.
Doyle, R.E., Vidal, S., Hinch, G.N., Fisher, A.D., Boissy, A., Lee, C., 2010. The effect of repeated testing on judgement biases in sheep. Behav. Processes 83, 349–352.
Fiset, S., 2007. Spatial memory in domestic dogs: Encoding of multiple cues for finding disappearing objects. Can. J. Exp. Psychol. 61, 350.
Fiset, S., Gagnon, S., Beaulieu, C., 2000. Spatial encoding of hidden objects in dogs (Canis familiaris). J. Comp. Psychol. 114, 315–324.
Harding, E.J., Paul, E.S., Mendl, M., 2004. Animal behavior - Cognitive bias and affective state. Nature 427, 312.
Head, E., Callahan, H., Muggenburg, B.A., Cotman, C.W., Milgram, N.W., 1998. Visual-discrimination learning ability and beta-amyloid accumulation in the dog. Neurobiol. Aging 19, 415–425.
Jonasson, Z., 2005. Meta-analysis of sex differences in rodent models of learning and memory: a review of behavioral and biological data. Neurosci. Biobehav. Rev. 28, 811–825.
Karagiannis, C.I., Burman, O.H.P., Mills, D.S., 2015. Dogs with separation-related problems show a "less pessimistic" cognitive bias during treatment with fluoxetine (Reconcile (TM)) and a behaviour modification plan. BMC Vet. Res. 11, 80.
Lazarowski, L., Foster, M.L., Gruen, M.E., Sherman, B.L., Case, B.C., Fish, R.E., Milgram, N.W., Dorman, D.C., 2014. Acquisition of a visual discrimination and reversal learning task by Labrador retrievers. Anim. Cogn. 17, 787–792.
Macpherson, K., Roberts, W.A., 2010. Spatial Memory in Dogs (Canis familiaris) on a Radial Maze. J. Comp. Psychol. 124, 47–56.
Marrs, W., Kuperman, J., Avedian, T., Roth, R.H., Jentsch, J.D., 2005. Alpha-2 adrenoceptor activation inhibits phencyclidine-induced deficits of spatial working memory in rats. Neuropsychopharmacology 30, 1500–1510.
Mendl, M., Brooke, J., Basse, C., Burman, O., Paul, E., Blackwell, E., Casey, R., 2010. R Dogs showing separation-related behaviour exhibit a 'pessimistic' cognitive bias. Curr. Biol. 20, R839–R840.
Mendl, M., Burman, O.H.P., Parker, R.M.A., Paul, E.S., 2009. Cognitive bias as an indicator of animal emotion and welfare: Emerging evidence and underlying mechanisms. Appl. Anim. Behav. Sci. 118, 161–181.
Milgram, N.W., 2003. Cognitive experience and its effect on age-dependent cognitive decline in beagle dogs. Neurochem. Res. 28, 1677–1682.
Milgram, N.W., Adams, B., Callahan, H., Head, E., Mackay, B., Thirlwell, C., Cotman, C.W., 1999. Landmark discrimination learning in the dog. Learn. Mem. 6, 54–61.
Milgram, N.W., Head, E., Weiner, E., Thomas, E., 1994. Cognitive functions and aging in the dog - acquisition of nonspatial visual tasks. Behav. Neurosci. 108, 57–68.
Mogg, K., Bradbury, K.E., Bradley, B.P., 2006. Interpretation of ambiguous information in clinical depression. Behav. Res. Ther. 44, 1411–1419.
Neave, H.W., Daros, R.R., Costa, J.H.C., von Keyserlingk, M.A.G., Weary, D.M., 2013. Pain and pessimism:Dairy calves exhibit negative judgement bias following hot-iron disbudding. PLoS One 8, e80556.
Sherman, B.L., Gruen, M.E., Case, B.C., Foster, M.L., Fish, R.E., Lazarowski, L., Depuy, V., Dorman, D.C., 2015. A test for the evaluation of emotional reactivity in Labrador retrievers used for explosives detection. J. Vet. Behav.:Clin. Appl. Res. 10, 94–102.
Tapp, P.D., Siwak, C.T., Estrada, J., Head, E., Muggenburg, B.A., Cotman, C.W., Milgram, N.W., 2003. Size and reversal learning in the beagle dog as a measure of executive function and inhibitory control in aging. Learn. Mem. 10, 64–73.
Yhnell, E., Dunnett, S.B., Brooks, S.P., 2016. The utilisation of operant delayed matching and non-matching to position for probing cognitive flexibility and working memory in mouse models of Huntington's disease. J. Neurosci. Methods 265, 72–80.