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Cognitive bias and paw preference in the domestic dog, *Canis familiaris*

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Abstract

Limb use, an indicator of hemispheric functioning, may be a useful predictor of cognitive bias and hence vulnerability to welfare risk. The relationship between cognitive bias and motor asymmetry, however, has been subject to little investigation. This study explored the association between motor asymmetry and cognitive bias in the domestic dog, a species that displays lateral bias in the form of paw preferences and exhibits positive and negative affective states. Thirty pet dogs had their paw preferences assessed using the Kong™ ball test. The subjects' affective state was assessed using a cognitive bias test in which the animals' latency to approach a bowl placed in one of three ambiguous positions was recorded. Animals veering more towards a left-paw preference were found to be significantly slower to approach the bowl placed in one of the ambiguous positions than ambilateral or right-pawed dogs. Left-pawed subjects approached the bowl located at the 3 ambiguous positions at roughly the same speed, while ambilateral and right-pawed animals became increasingly slower to approach the bowl the further it was located from the baited food bowl. The study points to a possible relationship between cognitive bias and paw preference in the dog, with left-pawed animals being more negative or “pessimistic” in their cognitive outlook than right-pawed or ambilateral individuals. It is proposed that limb preference testing might offer a more practical and straightforward way of identifying individuals at risk from poor welfare by virtue of how they perceive the world than more time-consuming cognitive bias tests.

Keywords: Animal welfare; Cognitive bias; Dogs; hand preference; judgement bias; lateral bias

1. Introduction

Research has drawn attention to the importance of considering an animal's affective state when assessing its welfare (e.g., Dawkins, 1990). Unfortunately, emotional states are highly subjective and, as such, cannot be measured directly in animals (Dawkins, 1993). A wide range of methods (e.g., studies of abnormal behaviour, physiological stress responses) have been used over the years in an effort to measure mammalian affect indirectly, although most have their limitations (for review Paul, Harding & Mendl, 2005).

Cognitive bias measures, which are designed to detect the valence of affective states, have recently been proposed as a promising new tool to assess animal emotions and potential welfare risk (e.g., Marchant-Forde, 2015; Mendl, Burman, Parker & Paul, 2009). Cognitive bias is a concept that was originally devised to explain human behaviour (Haselton & Nettle, 2006). The premise behind the paradigm is that cognitive processes, including attention, judgement and/or memory are influenced by affective state. Individuals harbouring a negative state of mind are more likely to attend to aversive stimuli, recall more negative memories and judge ambiguous stimuli as more negative than individuals with a more positive affective state (Paul et al. 2005; Mendl et al. 2009; Mendl, Brook, Basse, Burman, Paul et al. 2010). Cognitive bias tasks have been used successfully in an effort to shed light on the affective state and welfare of a wide range of animals [for reviews see Bethell, 2015; Roelofs, Boleij, Nordquist & van der Staay, 2016), including rats (e.g., Harding, Paul & Mendl, 2004), birds (Bateson & Matheson, 2007; Matheson, Asher & Bateson, 2008), sheep (e.g., Destrez, Deiss, Levy, Calandreau, Lee, Chaillou-Sagon et al. 2013) and, of pertinence to this paper, dogs (Burman, McGowan, Mendl, Norling, Paul, Rehn et al. 2011; Mendl et al. 2010; Titulaer, Blackwell, Mendl & Casey, 2013).

An animal's tendency towards a positive or negative cognitive bias appears to be related to dominance of the left or right cerebral hemisphere (Rogers, 2010). The two hemispheres differ significantly in their functions, including emotional processing, although there is still debate as to the exact contribution of each hemisphere in this role (for reviews see Davidson, 1995; Demaree, Everhart, Youngstrom & Harrison, 2005; Vallortigara & Versace, 2017]. The valence hypothesis (Davidson, 1995) proposes that the right hemisphere is responsible for the processing of fearful information, encouraging withdrawal from novel stimuli and situations (e.g., Rogers, Vallortigara & Andrew, 2013). The left hemisphere, by contrast, largely inhibits fear, encouraging exploration and approach behaviour (e.g., Silbermann & Weingartner, 1986). Dominance, or more frequent use, of one hemisphere over the other predisposes individuals to behave in a certain way, with left-handed or weakly lateralised individuals being more fearful than right-handed or strongly lateralised individuals (e.g., Rogers, 2010; Versace & Vallortigara, 2015). Limb preference (i.e., the preferred use of one hand/paw to perform a task) is associated with greater activity of the contralateral motor cortex (Versace & Vallortigara, 2015). Thus, the observation of a bias in hand (or paw) use can be considered an indicator of brain laterality (Batt, Batt, & McGreevy, 2007; Branson & Rogers, 2006; Gordon & Rogers, 2010; Hopkins & Bennett, 1994; Marshall-Pescini, Barnard, Branson & Valsecchi, 2013). Left-limbed animals, which tend to be right-hemisphere dominant, show stronger fear responses than right-limbed animals, which tend to be left-hemisphere dominant (e.g., Braccini & Caine, 2009; Cameron & Rogers, 1999). Left-sided biases of aggression, reactivity to fear-inducing stimuli and vigilance behaviour have also been noted in numerous species (e.g., amphibians-Lippolis, Bisazza, Rogers & Vallortigara, 2002; birds-Koboroff, Kaplan & Rogers, 2008, Zappia & Rogers, 1983; rats-Denenberg, 1984; horses-Austin & Rogers, 2012, Siniscalchi, Padalino, Lusito & Quaranta, 2014), including dogs (e.g., Siniscalchi, Lusito, Vallortigara & Quaranta, 2013; Quaranta,

Siniscalchi & Vallortigara, 2007; Quaranta, Siniscalchi, Frate, Iacoviello, Buonavoglia, & Vallortigara, 2006).

It has been proposed that limb use, a good indicator of hemispheric functioning (Annett, 1985; Springer & Deutsch, 1989), may be a useful predictor of cognitive bias and hence vulnerability to welfare risk (Rogers, 2010; Versace & Vallortigara, 2015). In the first, and only, study of its kind to explore this, Gordon and Rogers (2015) reported that left-handed marmosets were more likely than their right-handed counterparts to exhibit a negative cognitive bias, and concluded that hand preference, which can be easily measured, could be a straightforward and useful way of assessing welfare risk. Further work is clearly needed to examine the relationship between limb use and judgement bias, firstly to determine whether motor asymmetry is a variable that needs to be controlled for in cognitive bias studies, and, secondly, to establish whether limb use can be used in place of more timely cognitive bias tests as a reliable way of assessing animal welfare risk.

The following study examines the relationship between motor asymmetry and cognitive bias in the domestic dog, a species that has been shown to display both lateralised motor bias in the form of paw preferences (e.g., Branson & Rogers, 2006; Marshall-Pescini et al. 2013; Wells, 2003; Wells, Hepper, Milligan & Barnard, 2016) and exhibit positive and negative affective states as assessed by cognitive bias tests (Burman et al. 2011; Mendl et al. 2010; Titulaer et al. 2013) and other measures, e.g. approach-withdrawal responses, asymmetric tail-wagging, cardiac activity (Siniscalchi, Lusito, Vallortigara & Quaranta, 2013; Quaranta, Siniscalchi & Vallortigara, 2007). It is anticipated that the study will shed useful light on the relationship between limb use and emotional functioning in the dog, and, importantly,

establish whether motor asymmetry can be used as a reliable tool for assessing affective state in a species prone to welfare risk.

2. Methods

2.1. Subjects

Thirty pet dogs (13 males, 17 females) of mixed breed were recruited via response to an email advertising a study on paw preferences sent to pet owners in Northern Ireland, UK. The vast majority of the animals (n=27, 90%) were castrated. Animals ranged from 1 to 10 years of age (mean age=4.47 \pm SEM 0.47 years). All of the dogs were family pets living in households, and whose owners had consented to them taking part in the study. None of the dogs had undergone any behavioural training, nor had any disability preventing them from completing the study.

2.2. Paw Preference Testing

2.2.1. Apparatus

The subjects' paw preferences were tested using a Kong™ ball (KONG Company, Golden, CO, USA), the most commonly employed method of assessing motor asymmetry in the domestic dog (Batt, Batt & McGreevy, 2007; Batt, Baguley & McGreevy, 2008; Branson & Rogers, 2006; Marshall-Pescini et al. 2013; Schneider, Delfabbro & Burns, 2013; Tomkins, Thomson & McGreevy, 2010; Wells et al. 2016). A medium-sized Kong™ ball was used for testing. This is a hollow 10.5cm long conical-shaped rubber toy that moves in an erratic manner. The ball has a 2.9cm diameter hole at one end, and a smaller 1cm diameter hole at the opposite end. Before testing, the toy was filled through the larger hole with moist dog food (Pedigree, original flavour, Waltham Mars, UK) and frozen. Balls were washed thoroughly in between tests.

2.2.2. Procedure

Each dog was tested individually in its own home environment, on a hard-surfaced floor (tiled or linoleum), having been food deprived for at least 4 hours. At the start of testing, the dog was shown, and allowed to sniff, the food-loaded Kong™ ball. The toy was then placed directly in front of the animal. The paw used to stabilise the Kong™ by the dog was recorded by the experimenter. A paw use was classified as the animal having one or both paws on the Kong™ ball, regardless of duration. A separate paw use was considered to have been made when the animal removed its paw from the Kong™ and replaced one or both of its paws on the object. On occasion, dogs used both paws to stabilise the ball; these occurrences were recorded, but testing was not considered complete until one hundred paw uses (left plus right combined) had been made by the animal, regardless of the number of times dogs employed both paws.

2.3. Cognitive bias testing

The affective state of the subjects was assessed one month (+/- 3 days) following paw preference testing using a cognitive bias test modelled on that described by others (Burman et al. 2011; Mendl et al. 2010). Good test-retest reliability has been demonstrated in dogs tested with the Kong ball on 2 separate occasions, with an interim of 6 months between tests (Branson & Rogers, 2006), so it was assumed that the subjects' paw preferences would be consistent at the time of cognitive bias testing. All testing took place in an 8x7m room in the Animal Behaviour Centre, Queen's University Belfast, UK.

2.3.1. Training

Dogs were initially trained to learn the position of a bowl containing a food treat (Positive, P) and the position of a bowl devoid of food (Negative, N). The dog was held on a lead by its owner, while the Experimenter (SB) either placed a food treat (one cube of Frolic, Pedigree, Waltham Mars, UK) into the positive bowl (P) or set down an empty bowl (N). The bowl was tapped twice as a baiting signal (so the animal's performance was not influenced by hearing or not hearing the treat hit the bowl) and the Experimenter then said 'ok'; at this point, the subject was released from its starting point (4m away), midway between P and N (see Figure 1). The Experimenter consistently stood at the middle of furthest wall in the room, given that dogs can show lateralized responses upon seeing humans (Guo, Meints, Hall, Hall & Mills, 2009). Dogs initially received two consecutive positive trials (i.e., with the baited bowl placed in the P position), followed by 2 consecutive negative trials (i.e., with the un-baited bowl placed in the N position). Dogs were subsequently presented with positive and negative trials in a consistent, predefined order. No more than two trials of the same type were presented consecutively. P bowls were placed on the left-hand side of the room for 50% of the dogs, and on the right-hand side for the remainder of the subjects. For each dog, the latency to make contact with (i.e., touch or put its head inside) the bowl was recorded. A trial was terminated once the dog made contact with the bowl or 30 seconds had elapsed without the animal approaching the bowl. Each dog received a minimum of 15 training trials. Dogs were considered to have learned an association between the location of the bowl and its status (i.e., baited, P or un-baited, N) when, for the preceding three positive trials and the preceding three negative trials, the longest latency to reach the positive location was at least half a second shorter than any of the latencies to reach the negative location. Each dog was allowed a maximum of 50 trials to reach the criterion.

2.3.2. Testing

The testing phase commenced immediately following successful training to criterion. Dogs were presented with a food bowl placed in one of 3 different positions (Figure 1) between the original positive (P) and negative (N): (1) near-positive, NP; here the bowl was positioned one third of the way along from P; (2) Middle, M; here the bowl was placed mid-way between P and N, and (3) near negative, NN; here the bowl was placed one third of the way along from N. Dogs started each trial 4m away from the bowl at the mid-point between P and N as per training. Dogs were exposed to three test trials per location (i.e., nine test trials in total) in the order: 1) M, NP, NN; 2) NP, NN, M; 3) NN, M, NP. Test trials were separated from each other by 4 trials identical to those used in training to ensure dogs maintained their memory of the P and N locations. For each dog, the mean latency to make contact with the presented bowl was calculated as per the training trials.

Following testing, an empty food bowl was placed in the positive location. The aim of this was to check that dogs ran as quickly to this empty bowl as to the baited bowl in this location and hence were not relying on olfactory cues to guide behaviour.

(Figure 1 about here)

2.4. Data Analysis

2.4.1. Paw-preferences

Binomial z -scores were calculated to determine whether the frequency of right- or left-paw use exceeded that expected by chance. An alpha value of 0.05 was adopted for all analyses.

A z -score greater than +1.96 (two-tailed) reflected a significant left paw preference, whilst a z -score less than -1.96 indicated a significant right paw preference. Dogs with z -scores between +1.96 and -1.96 were classified as ambilateral.

A one-way chi-squared analysis was carried out to investigate whether there was a significant difference in the distribution of the dogs' paw preferences. Binomial tests were also conducted to determine whether there was a significant difference in the number of animals that were: (1) paw-preferent (either to the left or right) *vs.* ambilateral, and; (2) right- *vs.* left-paw preferent. Given the reported link between paw preferences and canine sex (McGreevy, Brueckner, Thomson & Branson, 2010; Quaranta, Siniscalchi, Frate & Vallortigara, 2004; Wells, 2003), chi-squared tests were carried out to establish whether the distribution of the dogs' paw use was associated with the subjects' sex (male, female).

A directional handedness index (HI) was calculated to quantify each dog's paw preference on a continuum from strongly left-paw preferent (+1) to strongly right paw-preferent (-1). The HI was calculated by dividing the difference between the total number of left and right paw reaches by their sum $(L-R)/(L+R)$ [see 34]. The strength of the dogs' paw preferences was calculated by taking the absolute value of each HI score (ABS-HI).

2.4.2. Cognitive bias

A series of non-parametric statistics was carried out to explore how long it took the subjects to reach the criterion for testing and to establish whether this was related to the animals' paw preference classification (left, right, ambilateral) or sex (male, female). A Kruskal-Wallis test was carried out to examine whether the dogs' latency to reach the empty food bowl

placed in the positive location differed significantly from their latency to reach the baited bowl.

For those animals that reach the criterion for testing, a Friedman test was carried out to determine whether the dogs' latency to reach the food bowl varied according to its position (P, NP, M, NN, N).

2.4.3. The relationship between paw preference and cognitive bias

Since the dogs recruited for this study differed in their size, each animal's test trial latencies were adjusted as per Mendl et al. (2010) to ensure results were not simply due to between-subjects differences in running speeds. The adjusted score was calculated in the following manner: $(\text{mean latency to probe location [i.e., NN, M or NP]} - \text{mean latency to positive location}) / (\text{mean latency to negative location} - \text{mean latency to positive location}) \times 100$. This adjustment resulted in the latencies to reach the bowls positioned in each of the 3 ambiguous locations being expressed as a percentage of the difference between each animal's mean latencies to reach the bowls positioned at P and N.

Kruskall-Wallis tests were carried out to explore whether there was relationship between the dogs' latency to approach bowls located at P and N (using unadjusted raw scores) or the three ambiguous locations (i.e., NP, M, NN, using adjusted scores). Friedman tests were subsequently conducted for left, right and ambilateral animals to determine if their speed to approach the three ambiguous bowls differed according to location.

Pearson moment correlations were carried out to examine the relationship between the direction (HI) and strength (ABS-HI) of the dogs' paw preferences and their latency to reach the bowls positioned at each of the 3 ambiguous locations (NP, M, NN).

Finally, independent *t*-tests and Mann-Whitney U tests were conducted to determine the relationship between the dogs' latency scores and canine sex.

Ethical approval

All methods adhered to the Association for the Study of Animal Behaviour/ Animal Behavior Society Guidelines for the Use of Animals in Research (Association for the Study of Animal Behaviour, 2006). Ethical approval for the study was granted by the Research Ethics Committee, School of Psychology, QUB.

3. Results

3.1. Paw preferences

The distribution of the dogs' paw preferences was not significantly different from that expected by chance alone, $\chi^2(2, N=30)=1.80, p=.41$). Seven (23.33%) dogs consistently used their left paw to balance the Kong™ ball, 10 (33.33%) consistently employed their right paw, while 13 animals (43.33%) were ambilateral. Dogs were no more likely to be paw-preferent ($N=17, 57.0%$) than ambilateral ($N=13, 43%$) [$p=.58$, binomial test]. There was no significant difference in the number of animals that were right- vs. left-paw preferent ($p=.63$, binomial test). Distribution of paw use was not significantly associated with canine sex, $\chi^2(2, N=30)=0.71, p=.70$).

3.2. Cognitive bias

3.2.1. Training

All of the dogs successfully completed the cognitive bias training, with animals reaching criterion after an average of 24.10 ($\pm 95\%$ C.I. 21.23-27.43) attempts. A Kruskal-Wallis test revealed no significant difference in the number of trials taken to reach criterion by ambilateral (mean number of trials=22.62 $\pm 95\%$ C.I. 19.62-25.77), right- (mean number of trials=25.30 $\pm 95\%$ C.I. 19.00-33.40), or left- (mean number of trials=25.14 $\pm 95\%$ C.I. 20.43-29.57) pawed dogs, $\chi^2(2, N=30)=0.71, p=.70$). Male and female dogs did not differ significantly in the number of trials required to reach criterion ($U=151.00, p=.09, r=.31$). The position of the positive (P) bowl (i.e., on the left- or right-hand side of the room) had no significant effect on the dogs' reaching criterion ($U=108.00, p=0.89, r=.03$).

It was concluded that all of the subjects successfully learned the cognitive bias task.

3.2.2. Testing

A Friedman test revealed a highly significant difference in the dogs' latency to reach the food bowl depending upon its position ($\chi^2(4)=90.03$, $N=30$, $p<.001$). Animals became increasingly slower to reach the bowl the further it was located from position P (see Figure 2).

(Figure 2 about here)

3.3. The relationship between paw preference and cognitive bias

Kruskal-Wallis tests revealed no significant relationship between the dogs' paw preferences and their latency to approach the food bowl located at either the Negative, N ($\chi^2(2)=.02$, $N=30$, $p=.99$) or Positive, P ($\chi^2(2)=1.57$, $N=30$, $p=.46$) position during the test trials (unadjusted raw scores, see Table 1). There was equally no significant association between the dogs' paw preferences and the speed with which they approached the food bowls located at NN ($\chi^2(2)=2.05$, $N=30$, $p=.36$), M ($\chi^2(2)=2.15$, $N=30$, $p=.34$) or NP ($\chi^2(2)=3.26$, $N=30$, $p=.20$) [Figure 3]. However, both right-pawed ($\chi^2(2)=7.40$, $N=30$, $p=.02$, $W=.37$) and ambilateral ($\chi^2(2)=22.15$, $N=30$, $p<0.001$, $W=.85$) dogs differed significantly in their latency to approach the 3 ambiguous food bowls, becoming increasingly slower the further the bowl was positioned from P. Left-pawed animals, by contrast, showed no significant difference in their latency scores for the bowls positioned at the 3 ambiguous locations ($\chi^2(2)=3.71$, $N=30$, $p=.16$) [Figure 3].

(Table 1 about here)

(Figure 3 about here)

Analysis revealed a highly significant positive correlation between the dogs' HI scores and their latency to approach the food bowl positioned at NP ($r(30)=.66, p<0.001$). Animals became slower to reach the bowl located in this position with increasing left-pawedness (Figure 4). Two outliers were visible on the scattergram and confirmed using the outlier labelling rule (Hoaglin & Iglewicz, 1987); the analysis was therefore re-run without these two datapoints. The dogs' HI Scores and latency to reach the bowl located at NP were still found to be positively correlated ($r(28)=.48, p=.01$); the removed datapoints were therefore not considered to be bivariate outliers. There was no significant correlation between the dogs' directional pawedness scores and their latency to reach the food bowl located at NN ($r(30)=-.28, p=.14$) or M ($r(30)=.01, p=.96$).

(Figure 4 about here)

The strength of the dogs' paw preferences (ABS-HI) was significantly correlated with their speed to reach the food bowl located at NP ($r(30)=0.39, p=.03$). Animals became slower to reach the bowl at this location with increasing lateralisation (Figure 5). The strength of the dogs' paw preferences was not significantly correlated with their latency scores for bowls located at NN ($r(30)=.16, p=.40$) or M ($r(30)=.20, p=.29$).

(Figure 5 about here)

3.4. The effect of canine sex on paw preference and cognitive bias

Analysis revealed no significant effect of canine sex on either the direction ($U=99.50, p=.65, r=.08$) or strength ($U=106.50, p=.87, r=.03$) of the animals' paw preferences. There was no

significant difference in the latency scores of male and female dogs for the food bowl located at NN ($U=72.0$, $p=.11$, $r=.29$), M ($U=87.00$, $p=.32$, $r=.18$) or NP ($U=109.00$, $p=.95$, $r=.01$).

3.5. Latency to reach the empty food bowl

Dogs showed no significant ($Z=-.30$, $p=0.76$) difference in their latency to approach the empty food bowl placed in the positive location (P) and the baited bowl. Latency to approach the empty food bowl placed at P was not significantly related to the animals' paw preference classification ($\chi^2(2)=.24$, $N=30$, $p=.89$) or canine sex ($U=85.50$, $p=.30$, $r=.19$).

4. Discussion

This study aimed to examine, for the first time, the relationship between motor asymmetry and cognitive bias in the domestic dog. The findings from the investigation point to a relationship between these two phenomena.

The results from this study revealed a roughly equal distribution of lateralised (57%) and non-lateralised (43%) dogs as assessed using the Kong ball test; there was therefore no evidence of a population-level bias. Existing research on the distribution of paw preferences in dogs is conflicting, with some studies highlighting a higher percentage of lateralised than non-lateralised animals (e.g., 75% lateralised [Tan 1987]; 77% lateralised [Branson & Rogers, 2006]; 79% lateralised [Siniscalchi et al. 2008], and others showing more of an equal distribution of ambilateral and paw-preferent individuals (46% lateralised [Marshall-Pescini et al. 2013]; 37% lateralised [McGreevy et al. 2010]; 52% lateralised [Tomkins et al. 2010]). The results from the present investigation add to the conflict, but are more in line with those studies pointing to a roughly equal split of lateralised and non-lateralised dogs. It is likely that differences in sample constitution (e.g. sex split, castration status), task complexity and other, uncontrolled for, variables (e.g. experimenter handedness), contribute towards this discrepancy in results in dogs, in much the same way as they do in other species (see Rogers, 2009; Strockens, Gunturkun & Ocklenburg, 2013; Versace & Vallortigara, 2015).

The dogs in this study were all successfully trained to criterion and performed as expected on the cognitive bias test, becoming increasingly slower to approach the food bowl the further it was located from the baited position (P). Although the dogs' paw preference classification (i.e., left, right, ambilateral) was not significantly related to their latency to approach the food bowls positioned in any of the locations, analysis did reveal a significant positive correlation

between the latency of dogs to approach the Near Positive (NP) bowl and their directional pawedness (HI) scores. Dogs became increasingly slower to approach the bowl located at NP with increasing left-pawedness. As indicated earlier, the right hemisphere is generally considered to be responsible for the processing of fearful information, encouraging withdrawal from novel stimuli and situations (e.g., Rogers et al. 2013). Left-limbed individuals, which are more right-hemisphere dominant, are therefore more likely to be fearful and prone to maladaptive behaviour than their right-limbed counterparts.

One explanation for the results observed here is that the dogs with left-paw preferences were more “pessimistic” (i.e., negative) in their cognitive bias. Mendl and colleagues (2010) found that dogs with higher separation-related behaviour (SRB) scores displayed a more “pessimistic” judgement of ambiguous test locations (M and NN) than animals with lower SRB scores, using the same experimental paradigm adopted here. More recently, Gordon and Rogers (2015) found that left-handed marmosets were less likely to remove the lid of an ambiguous food bowl than their right-handed counterparts. In the present study, the bowl located at NP, although ambiguous in nature, was more likely to contain a food treat than a bowl located further away from P, and one would therefore have expected animals to have displayed relatively low latencies to approach the bowl positioned in this location. The left-pawed dogs in this study, however, were slower to approach NP than their ambilateral or right-pawed counterparts; it could therefore be argued that these animals were more likely to perceive the bowl located in this position as unloaded, than loaded, with food. Further support for this hypothesis comes from the finding that the left-pawed dogs approached the food bowl located at the 3 ambiguous positions (NP, M, NN) at roughly the same speed. Ambilateral and right-pawed animals, by contrast, showed a significant difference in their latencies across the three locations, becoming increasingly slower, as one would expect, the

further the bowl was located from P. Left-pawed dogs were certainly able to distinguish between the positive and negative food locations (as evidenced by their faster latencies to approach P than N), which increases the likelihood that they were able to perceive and understand the difference in the valence of the food bowls located in each of the ambiguous positions. The most likely explanation is that these animals simply adopted the more pessimistic outlook that food would not be available in any of the bowls, regardless of where it was positioned between P and N.

An intriguing alternative account for the above is that the left-pawed dogs in this study were more inflexible in their way of thinking than the right-pawed or ambilateral animals. Research from the human literature suggests that people with pervasive developmental disorders (e.g., Autism Spectrum Disorder), veer more towards left- than right-handedness (for review, Lindell & Hudry, 2013). There is a tendency for such individuals to be relatively ‘rigid’ in their outlook, finding it challenging to overlook minute details. Perhaps the left-pawed dogs in this study, as is often the case in people with atypical cortical organization, were more focused on the detail than their right-pawed or ambilateral counterparts, regarding all of the ambiguous bowls to be ‘incorrect’. Further work, perhaps exploring problem-solving strategies in left vs. right-pawed/ambilateral dogs, may help to elucidate whether there is any plausibility to this idea.

The strength of the dogs’ paw preferences was also found to be correlated with their latency to reach the bowl located at NP. The degree to which one hemisphere is dominant over the other may influence an individual’s reactivity to potential stressors (Rogers, Zucca & Vallortigara, 2004). Individuals with a more strongly dominant hemisphere may be better able

to deal with stress than those who do not rely on one hemisphere over the other (Branson & Rogers, 2006). For example, ambilateral chicks emit more distress calls in response to the sight of a predator than their more lateralised counterparts (Dharmaretnam & Rogers, 2005). In light of this, one might have expected the more strongly lateralised dogs in this study to have been faster to approach the ambiguous food bowls than those with weaker paw preferences. There were indeed individuals that displayed this pattern, but further work is needed to explore the relationship between strength of lateralisation and cognitive bias in domestic dogs before firm conclusions on this relationship can be drawn.

The results of this study revealed no significant effect of canine sex on any of the dependent variables under scrutiny, including distribution of paw use. This is interesting, since several studies have pointed to a relationship between paw preference and canine sex, with male animals veering more towards left-paw use and females showing more of a tendency to use their right paw (McGreevy et al. 2010; Quaranta et al. 2004; Wells, 2003). These studies, however, all used non-castrated animals as subjects. Other investigations, either using castrated, or a mixture of de-sexed and entire, animals have not reported a significant sex effect on dogs' paw preferences (Batt et al. 2008; Branson & Rogers, 2006; Schneider et al. 2012). This is more in keeping with our results, using a population of mostly (90%) neutered animals. It seems most likely that a hormonal factor is at play in explaining these disparate results (see Geschwind & Galaburda, 1985a, 1985b; Witelson, 1991). However, other, uncontrolled for, individual differences deserve attention. For example, laterality has been linked to personality in some species (e.g., fish-Brown & Bibost, 2014; cats-McDowell, Wells & Hepper, 2016). The relationship between temperament and lateral bias in dogs is still inconclusive (see Batt et al. 2009; Schneider et al. 2013), although our recent work points to a possible link (Barnard, Wells, Hepper & Milligan, in press).

While this study shows an association between cognitive bias and paw preferences in the dog, it does not enable us to draw any causal relationship between these two variables. Cats typically develop a stable paw preference by 1 year of age (Wells & Millsopp, 2012). It is still unknown at what age dogs develop a stable paw preference, however measuring the lateral and cognitive biases of such animals during their first year of life may help to establish whether paw preferences develop before or after cognitive bias. Care does need to be taken with this approach, however, since it is possible that training for cognitive bias may actually influence an animal's emotional state (see Bethell, 2015). Further work is certainly needed, ideally using larger numbers of subjects, to determine the causal mechanisms underlying preferred paw use in dogs and its complex relationship with other variables.

Conclusion

Cognitive bias tests have become an increasingly popular and influential way of assessing emotional functioning and the affective state of animals (Bateson & Nettle, 2015). Although clearly a useful tool for welfare assessment, the training involved in such tests is a time-consuming process, potentially stressful for social animals that require individual testing and not always practical for use in applied contexts, e.g., rescue shelters (see Roelofs et al. 2016). Assessing an animal's paw preferences, by contrast, is a quick and, in most cases, straightforward procedure from a methodological perspective. If paw preferences and cognitive bias are indeed related, then this opens the door for motor bias testing to be used as a quick and easy tool for assessing animals which might be at risk from reduced welfare by virtue of how they perceive the world (see Rogers, 2010). Identifying such individuals would then enable appropriate interventions to be put in place with the aim of improving animal well-being. For example, the rescue shelter environment is a highly stressful one for the many thousands of dogs around the globe that find themselves in this situation (see Wells,

2004 for review). Paw preference testing might be of use in this context, allowing kennel staff to identify animals at heightened risk from developing behavioural or physiological symptoms of stress. Beyond the kennel environment, paw preference tests could perhaps be used to identify animals that are more prone to developing behaviour problems symptomatic of anxiety, e.g., fear aggression, separation anxiety. Appropriate advice could then be given to potential adopters, highlighting the needs of the individual. Work is currently underway in an effort to shed further light on the relationship between cerebral functional asymmetry, emotional vulnerability and well-being in non-human animals.

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Figure Legends

Figure 1. Depiction of the food bowl positions used in the cognitive bias test (P=positive position [bowl baited with food]; NP=near positive; M=middle; NN=near negative; N=negative position [bowl devoid of food])

Figure 2. Mean latencies (\pm SEM) for dogs to reach the food bowl located at 5 separate positions

Figure 3. Mean adjusted latency (\pm SEM) scores for the food bowl located at three ambiguous places (NP, M, NN) according to the dogs' paw preference classification.

Figure 4. Scattergram showing the relationship between the dogs' HI (direction of paw use) scores and adjusted latency scores when presented with the Near Positive (NP) bowl

Figure 5. Scattergram showing the relationship between the dogs' ABS-HI (strength of paw use) scores and adjusted latency scores when presented with the Near Positive (NP) bowl

Table Legend

Table 1. The mean (+/-SEM) latency scores for ambilateral, right- and left-pawed dogs for food bowls positioned at the Positive (P) and Negative (N) location.

Figure 1

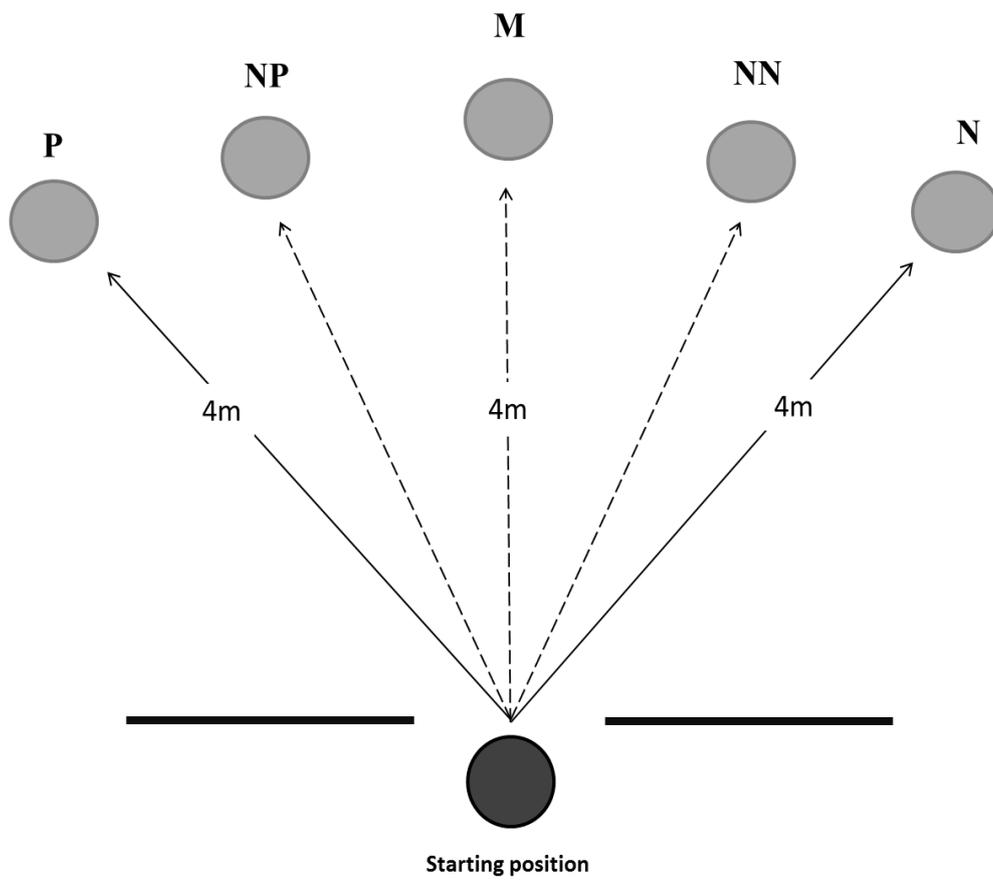


Figure 2

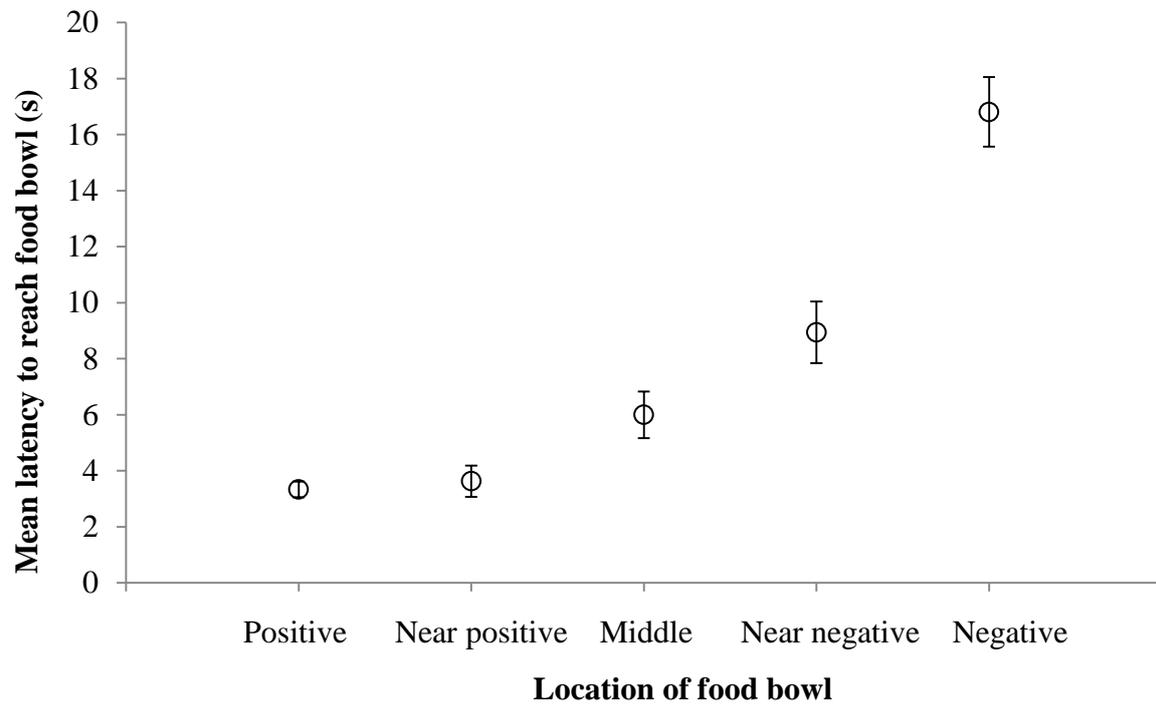


Figure 3

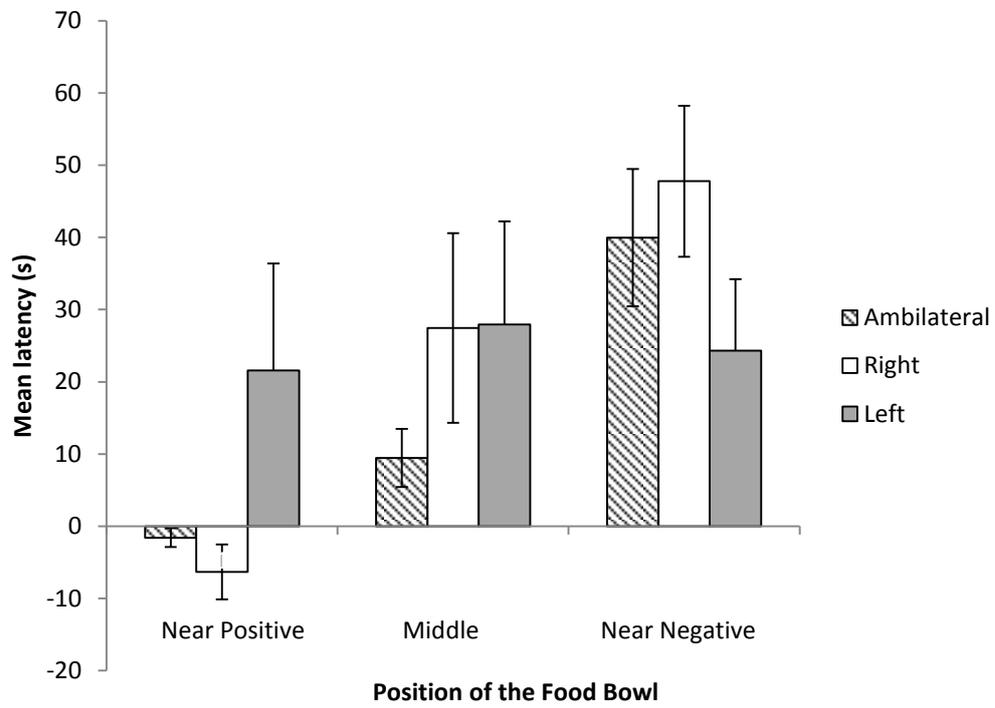


Figure 4

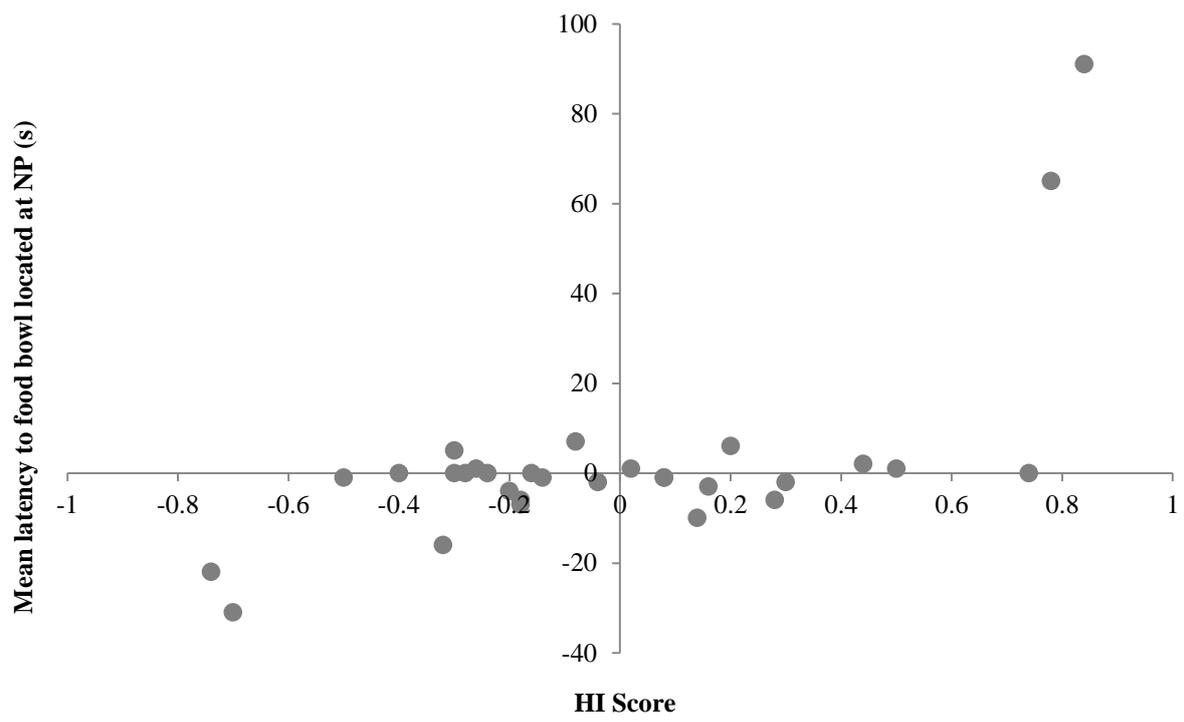


Figure 5

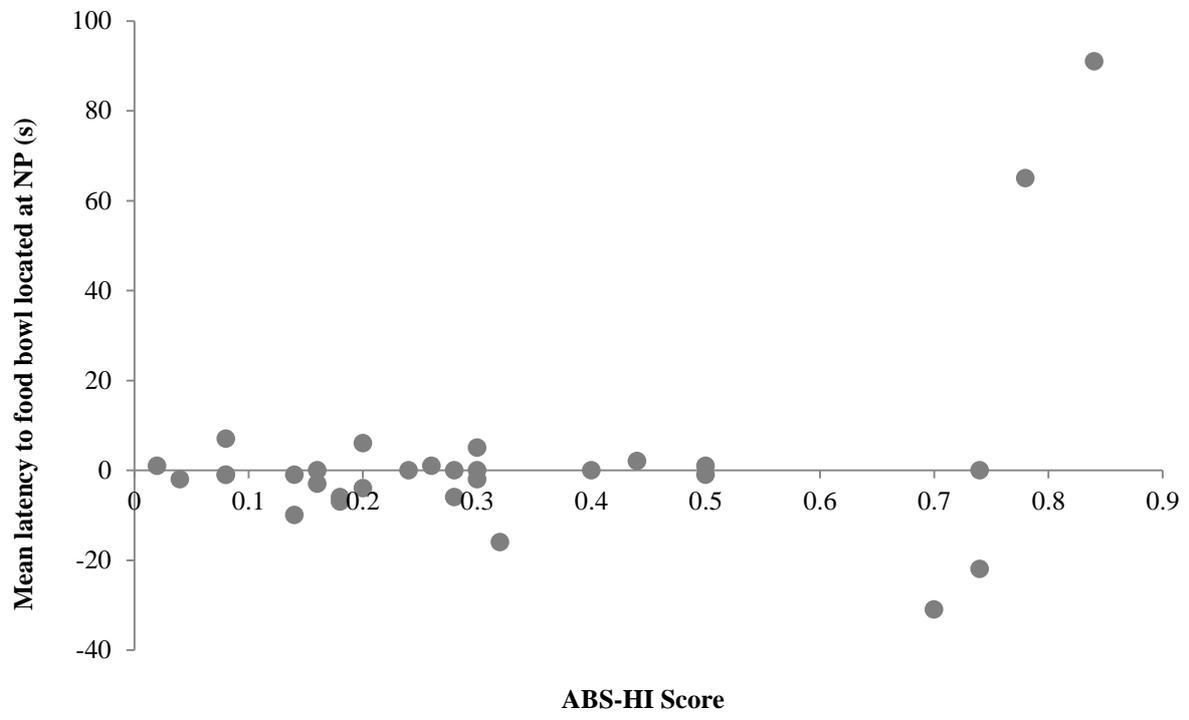


Table 1

Paw preference	Positive	Negative
	Mean (\pmSEM)	Mean (\pmSEM)
<i>Ambilateral</i>	3.26 (0.30)	17.03 (2.15)
<i>Right</i>	3.58 (0.60)	16.67 (2.23)
<i>Left</i>	3.15 (0.74)	16.62 (2.01)