

Dog paw preference shows lability and sex differences

Fay Poyser^a, Christine Caldwell^{b,1}, Matthew Cobb^{a,*}

^a Faculty of Life Sciences, University of Manchester, Manchester M13 9PT, United Kingdom

^b School of Psychology, Washington Singer Laboratories, University of Exeter, Exeter EX4 4QG, United Kingdom

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Abstract

Paw preferences in domestic dogs were studied using three different behavioural tests, recording frequency, duration and latency of paw use. No overall population tendency to right- or left-paw preference was seen on any of the tests, nor could a sub-population of handed dogs be detected. This failure to replicate previous reports that male dogs tend to use their left paws while females use their right was counterbalanced by a significant tendency for male dogs to use their left paw when initially presented with one test, and for the latency of left paw use to be significantly shorter than that for right paw use on these initial presentations. This significant effect disappeared with repeated presentation of the test, and was not present in females. We conclude that behavioural lateralisation appears to be a labile category in dogs, and may be related to brain hemispheric effects in responding to novel stimuli.

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Handedness exists in all modern human populations, with 90% of our species preferring to use their right hand for many complex behaviours (McManus, 2002). There is now a substantial amount of evidence to suggest that other vertebrates, in particular primates, show some level of lateralisation (Fagot and Vauclair, 1991; McGrew and Marchant, 1999; Rogers and Andrews, 2002). Over recent years, lateralised behaviour has been reported in, amongst many others, fish (Bisazza et al., 2001), octopuses (Byrne et al., 2004), snakes (Roth, 2003) and toads (Bisazza et al., 1996; but see Naitoh and Wassersug, 1996).

“Handedness” of varying kinds has also been reported in a number of non-primate quadruped mammals—rats (Collins, 1975; Glick and Ross, 1981), cats (Cole, 1955; Elalmis et al., 2003; Fabre-Thorpe et al., 1993; Pike and Maitland, 1997; Tan et al., 1990), horses (Murphy et al., 2005) and dogs (Tan, 1987; Quaranta et al., 2004; Wells, 2003). Some of these studies are inconsistent; for example, rats have been reported to be both right-handed (Glick and Ross, 1981), and left-handed (Collins, 1975), while cats have been reported to be right-handed (Tan et al., 1990) and to show a left-paw bias for striking a moving tar-

get (Fabre-Thorpe et al., 1993). One explanation for these varied findings may be the possibility that there are sex differences in lateralised behaviour shown by quadruped mammals. A series of consistent recent reports suggest this to be the case: Elalmis et al. (2003) reported strong right-handedness in female rats, Murphy et al. (2005) found that male horses tended to start movements with their left hoof while females used their right, while both Wells (2003) and Quaranta et al. (2004) reported a tendency for male dogs to be left-pawed. Any such sex differences may be due to differential hormonal effects on brain development, which have been widely linked to laterality effects in vertebrates (Rogers and Andrews, 2002).

However, on closer inspection, the two most recent studies on dog “handedness” suggest that the phenomenon of sex-linked lateralisation in this quadruped is not as solid as might first appear. Results from different tasks tend to lead to different conclusions. For example, Wells (2003) found the strongest tendency for male dogs to use their left paw in a test that involved the dog responding to a command (i.e. ‘give’ a paw), while there was no significant tendency for males to use their left paw in a test requiring the animal to remove a blanket from their head. Wells (2003) rightly pointed out that the findings of her study should not be generalised until an exploration of paw preferences in completely untrained dogs had been undertaken. Quaranta et al. (2004) used a similar “scratching” test to the blanket test used by Wells (2003), which required pet dogs to remove a piece of

* Corresponding author. Tel.: +44 161 275 5419; fax: +44 161 275 5082.

E-mail address: cobb@manchester.ac.uk (M. Cobb).

¹ Present address: Psychology Department, University of Stirling, Stirling FK9 4LA, United Kingdom.

tape from its nose. Although there was a clear tendency for males to prefer using their left paw, the converse right paw preference in females was barely significant ($p < 0.10$ in a one-tailed test).

This suggests that it would be appropriate to replicate these studies, in order to clarify whether there is a widespread sex difference in paw preference in dogs, and also to compare the results from different tests. To limit the proximal effects of any training, we studied the behaviour of stray and unwanted dogs in a dogs' home. We used three tests of lateralised behaviour, measuring paw preference in terms of frequency, duration and latency. Some of our findings confirm the existence of a sex difference in lateralisation of behaviour in the domestic dog, although indicating that it is not constant over time; our failure to replicate some previous measures indicates that this phenotype may not be particularly robust, and may be expressed in a variety of ways.

1. Materials and methods

1.1. Subjects

Seventy-nine stray or unwanted pedigree and mongrel domestic dogs (*Canis familiaris*), housed in the City Dogs' Home, Bucknall, UK, were studied. Thirty-six females (18 neutered, 18 intact) and 43 males (16 neutered, 27 intact) were studied. Because of the transient nature of this population (some dogs were re-homed during the experiment), some dogs could not be used in all tests. No difference was observed between neutered and intact dogs on any test, for either males or females. As the exact age of each dog was not known, young-looking dogs were not tested until they were certified as sexually mature. Dogs that might have been neutered before sexual maturity were not studied. Males were classed as sexually mature if they had no milk teeth and cocked their leg to urinate. Females were classed as sexually mature if they had no milk teeth and had apparently been through their first season (determined by examining their abdomen). Prior to their arrival in the dogs' home, some of these dogs may have spent their entire life in a domestic setting and have been highly trained, which could affect the validity of the behavioural measures (Wells, 2003). However, during testing the dogs would often run in circles barking; many of them repeatedly left the task or simply failed to start it, suggesting that any training effects upon the behaviour of the dogs were relatively weak in the conditions of the dogs' home. The dogs were housed and tested in individual kennels. Each kennel had an external concrete run (1.5 m × 3 m) with a wire mesh door and an internal tiled run (1.5 m × 3 m). The internal run had a wire mesh door that was used for observation by the researcher. During testing dogs had access to both sides of their kennel. Testing was done in the internal tiled run.

1.2. Procedure

1.2.1. General

Initial attempts were made to replicate two of the three measures used by Wells (2003) in her study of pet dogs—removal of a treat from a tin and removal of a blanket placed over the

head. The third measure used by Wells (2003) – “give paw”, which provided the strongest sex-differences in her study – was not considered. As she discussed, although it seems unlikely that owners will have trained males to give their left paw and females their right, this measure could nevertheless be confounded by learned, rather than constitutional, responses. Furthermore, it required the dog to engage in more complex interactions with the experimenter, which could also lead to artefacts. Unfortunately, neither of Wells' protocols we attempted to repeat – the tin and blanket tests – provided satisfactory data with our group of stray and unwanted dogs: they did not use their paws to remove the treat, and would back out from under the blanket rather than using their paws to remove it. We were therefore obliged to develop two novel tests of paw preference, which were employed together with a task that had been used by Quaranta et al. (2004). Our objective was to enable the dogs to provide a range of behavioural responses through which we could detect lateralisation of behaviour. In order to avoid the problems of human–animal interaction highlighted by Wells (2003), we attempted to ensure that the test procedures required as few interactions as possible. The experimenter was silent during all tests and no other human or dog was present.

1.2.2. Chew (Fig. 1a)

This test was designed to detect paw preference by measuring the total time each paw was used during food manipulation. The dog was provided with a raw hide chew, and its paw contacts with the chew were observed. The foot holding the chew down was defined as the “dominant” paw; if both paws were used to hold the chew between them, with neither paw on top, this was recorded as “both paws”. The duration of each contact of the dominant paw with the chew was recorded in seconds; this also allowed us to note the duration of the first use of each paw. Small dogs (<15" at shoulder) were presented with a 15 cm × 0.5 cm cylindrical raw hide chew, while larger dogs were presented with a 30 cm × 1 cm cylindrical raw hide chew. If the chews were ignored they were dipped in cod liver oil, natural yoghurt or congealed lamb fat and re-presented to the dogs. Chews were presented on consecutive days until six sessions had been recorded or the dogs continuously refused them. Each dog was observed for 4 min or until the chew was eaten. Sessions where the total time spent touching the chew <20 s were excluded from analysis (eight sessions were thus excluded, each for different dogs).

1.2.3. Tape (Fig. 1b)

This test was designed to detect paw preference by measuring the frequency with which each paw was used when removing an irritant placed centrally on the dog. The procedure was essentially that used by Quaranta et al. (2004): a 2 cm square piece of adhesive tape was stuck on the dog's nose while the dog was standing up. The first paw lifted to try and remove the tape was recorded and the tape was then removed. It was impossible for dogs to remove the tape with two paws. The (right-handed) observer used alternate hands to stick the tape on the dog's nose. No more than four tests were done each day, interspersed with other measures. Data collection continued on consecutive days until around 20 tests had been carried out or the dog became

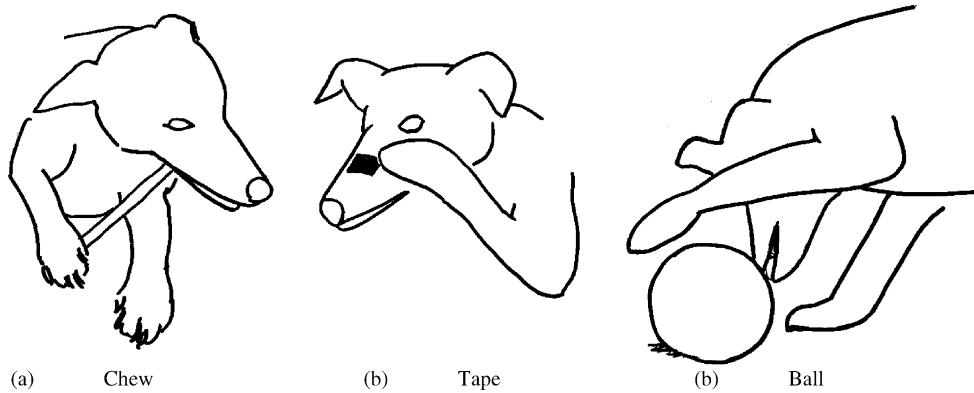


Fig. 1. Drawings of dogs in the three behavioural tests. For details of tests, see Section 1.

distressed. Only data from those dogs where >10 tests were obtained were included. As a result, the number of dogs ($n = 46$) tested in this procedure was smaller than that in the other two tests.

1.2.4. Ball (Fig. 1c)

This test was designed to detect paw preference by measuring the speed with which the dog began to use each paw when manipulating an interesting object, and was inspired by the procedure used by Fabre-Thorpe et al. (1993) in their study of lateralised behaviour in cats. A Winalot “Shapes” activity ball was filled with mixed dog treats and placed on the floor in front of the dog. When batted around the floor by the dog, treats would fall out at random, with an average frequency of about 1 treat for every 10 hits of the ball. Two measures were recorded: the latency of the first touch of the ball, as measured from the start of the test, and the paw used in the first and approximately 19 subsequent touches of the ball. A touch of the ball was recorded only if, prior to the touch, the dog was standing on all four paws. Dogs virtually never hit the ball with two paws at once; when this occurred the data point was discarded. To analyse the possibility that the receipt of a reward altered the subsequent paw used, all instances when a treat was recovered from the ball were noted. The paw used to recover a treat was then compared with the next paw that was used to touch the ball, in a χ^2 goodness-of-fit test for a random sample of 25 dogs. The receipt of a food reward did not significantly affect the paw that was used next ($\chi^2 = 2.205$, $p = \text{n.s.}$) and so the ball “hits” were classed as independent data points. The activity ball was presented to each dog once a day until six sessions had been recorded, the dog lost interest or was re-homed. Only those sessions with at least 10 hits, and only those dogs with at least 3 sessions, were included in the analysis.

1.3. Data analysis

For each measure of the frequency of paw use, a handedness index (HI) was calculated to quantify each dog’s paw preference on a continuum from completely left paw preferent (−1) to completely right paw preferent (+1) ($\text{HI} = (\text{frequency R} - \text{frequency L}) / \text{total frequency}$). For the chew test, which was based on time each paw was used, rather than frequency, $\text{HI} = (\text{total time R} - \text{total time L}) / (\text{total time R} + \text{L} + \text{both paws})$.

These indices provide a continuous measure of laterality, rather than classifying animals into two or three handedness categories on the basis of a threshold. Data were analysed using Statview and JMP statistics programmes.

2. Results

Frequency distributions of individual handedness indices (HI) for all three tests (Chew, Tape and Ball) are shown in Fig. 2. None of the distributions was significantly different from normal (Shapiro–Wilk test of normality: $W_{58} = 0.959$, $W_{34} = 0.984$ and $W_{53} = 0.969$, Chew, Tape and Ball respectively; $p = \text{n.s.}$ in all cases). A population-level handedness effect on these measures would have produced either a skewed or a U-shaped distribution. Comparison of HIs for males and females revealed no significant differences between the sexes for any of these measures ($t_{58} = 0.016$; $t_{34} = 0.503$; $t_{53} = 0.329$; $p = \text{n.s.}$ Chew, Tape and Ball, respectively). Intra-individual consistency in lateralisation was tested by calculating correlation coefficients between the three measures. One correlation was barely significant: Tape/Ball $r = 0.358$ ($n = 32$), $p = 0.044$; the other two were non-significant: Tape/Chew $r = 0.216$ ($n = 30$); Ball/Chew $r = -0.053$ ($n = 46$).

To detect whether the potential effect of a small number of lateralised dogs was swamped by a majority of ambidextrous individuals, correlations were calculated only for those dogs which showed at least one $\text{HI} > 0.4$ or < -0.4 . None of the correlations were significant: Tape/Chew $r = 0.226$ ($n = 19$); Ball/Chew $r = 0.051$ ($n = 25$); Tape/Ball $r = 0.436$ ($n = 12$), indicating that intra-individual consistency in lateralisation was no greater for animals with more extreme handedness indices. This initial exploration of the data suggests that these tests did not confirm previous reports of a tendency for dogs to show a behavioural lateral preference, nor did they provide evidence of a sex-difference in any such lateralisation of behaviour.

To further explore this apparent failure to replicate, we examined our most extensive data set, which was obtained from the Ball test and included data over six sessions on separate days, and studied whether there were any trends in the data. Fig. 3 shows the overall handedness of male and female dogs in their first contact with the ball on each of the six test sessions.

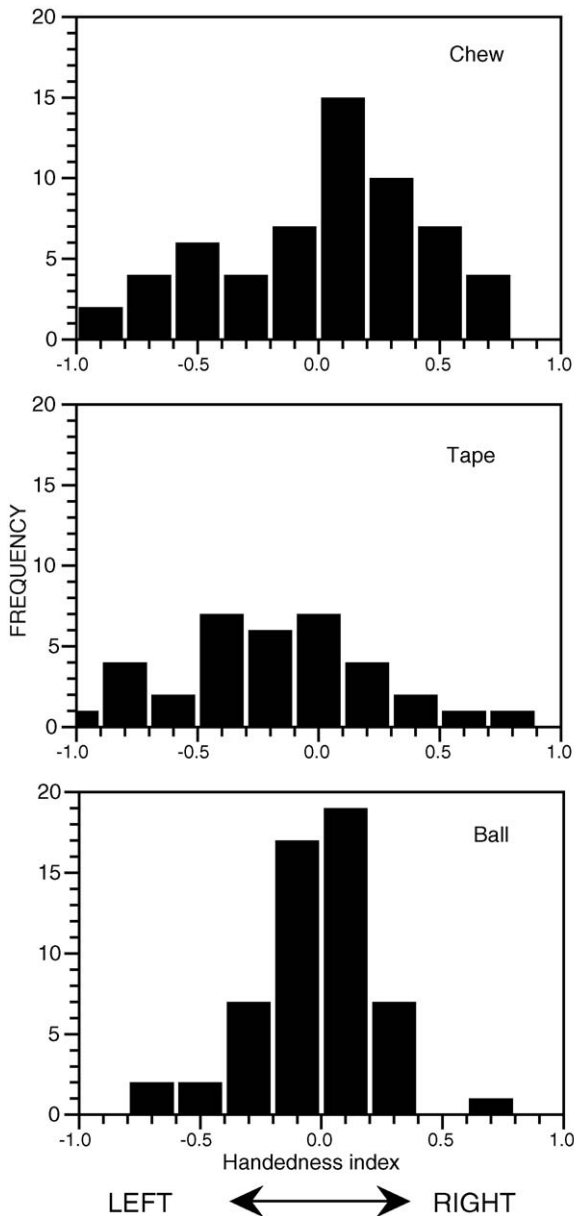


Fig. 2. Distribution of handedness scores for individual dogs in three behavioural tests. For details of tests, see Section 1.

There was a significant tendency for dogs to use their left paw to touch the ball on their first encounter with the ball (L=42, R=27, χ^2 goodness-of-fit=4.833, $p=0.028$), but this effect was produced entirely by male dogs: males L=24, R=14, χ^2 goodness-of-fit=6.647, $p<0.01$; females L=17, R=13 χ^2 goodness-of-fit=0.154, $p=n.s.$ This tendency for left-paw preference in males gradually declined over the six sessions with the ball (Fig. 3): male dogs showed a significant decline in their left paw preference with repeated presentations of the ball ($r=0.874, p<0.02$), while there was no significant change in the preference of females over the same period ($r=0.283, p=n.s.$).

There was also a significant left-right difference in the rapidity with which dogs struck the ball for the first time in each session, as measured by latency. For each dog, the difference in

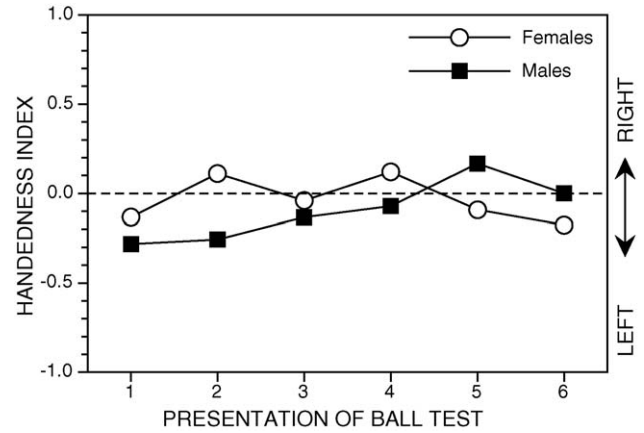


Fig. 3. Changes in population-level handedness of male and female dogs over test sessions, measured for the first touch of the ball.

the mean latency for first right paw use compared with its mean latency for first left paw use was calculated (dogs which always struck the ball first with the same paw ($n=11$) were excluded). Comparison of the difference scores with a theoretical distribution (mean = 0, no difference in paw latency) revealed a highly significant tendency for the left paw to be used more rapidly than the right paw ($t_{50} = 2.897, p < 0.006$). When the difference scores were separated by sex and each compared against the theoretical distribution, only male dogs showed a significant difference in paw latency: males $t_{25} = 2.74, p = 0.011$; females $t_{24} = 1.25, p = n.s.$ The same procedure was used to study differences in the duration of first left and right paw use in the Chew test; this revealed no significant difference between the two paws ($t_{59} = 0.372, p = n.s.$) and no sex difference ($t_{58} = 0.23, p = n.s.$).

To test whether the effect observed with the Ball test might be due to repeated presentation, differences in the latency to strike the ball on the first and last test were measured in all dogs, which performed the test on at least three occasions. Mean latency for the first strike of the ball in fact showed a significant decrease over trials ($F_{1,106} = 10.73, p = 0.014$), but there were no sex differences, nor was there any significant interaction with sex ($F_{1,106} = 2.47$ and 0.31 , respectively, $p = n.s.$), indicating that this effect cannot account for the observed sex differences in latency and tendency to left paw use.

3. Discussion

Our finding of a tendency for male dogs to prefer using their left paw on early presentations of the Ball test accords with previous reports suggesting male dogs show a left-handed preference (Quaranta et al., 2004; Wells, 2003). However, we also found that this tendency declined with repeated presentation, indicating that the phenotype is labile. It may also be affected by other factors: we found no lateralisation in first paw use in the Chew test. Our other measures strikingly failed to reveal sex differences in lateralisation of behaviour – or even evidence of consistent lateralisation. In particular, the fact that we did not observe any such effect on what was essentially the same measure as used by Quaranta et al. (2004) (removing

the tape from the nose) suggests that as well as being labile, the lateralisation phenotype in dogs may not be particularly robust.

A number of factors may explain our failure to find consistent lateralised behaviour, or sex differences for this effect. Firstly, the general difficulties associated with providing valid and reliable measures of animal behaviour are undoubtedly increased when studying dogs, which have individual and species-specific histories of close links with humans. The use of pet dogs (Quaranta et al., 2004; Wells, 2003) may reveal different aspects of behaviour compared with our use of unwanted and stray dogs. Furthermore, the particular conditions of a dogs' home may have led to lateralisation being masked by other behavioural responses (e.g. stress, excitement when faced with a novel situation). The fact that the behaviour of the dogs in our study made it impossible to replicate the test used by Wells (2003) in which a blanket was placed on the dog's head (the dogs did not use a paw to remove it, but instead backed out from the cover) suggests that our dogs were more active, or at least less "well behaved" in the presence of humans than the pets used in previous studies. However, as Wells (2003) indicated, the use of pet dogs raises a different set of problems—results from such animals may be affected by a potential "Clever Hans" effect, whereby the animal picks up subtle unconscious non-verbal cues from the experimenter and alters its behaviour accordingly. While the dogs studied here had the advantage of not being currently influenced by close human contact, they presented a difficulty in that their past experiences were unknown and almost certainly mixed.

A related difficulty flows from studying lateralised behaviour in animals that regularly interact with humans (e.g. in zoos, farms, laboratories or homes): these animals encounter a consistently lateralised environment that might lead to the expression of lateralised behaviour through learning rather than through a constitutional neurobiological lateralisation. Any such effects could be expected to be stronger in those animals living in a domestic environment, which provides many consistent lateralised cues in terms of the organisation of rooms and furniture, etc. Conversely, this kind of confounding effect might have been weaker in our stray and unwanted dogs, which, at the time of testing, were living in the relatively sparse environment of the dogs' home. Another possible explanation of the relatively weak evidence for lateralisation reported here is that the lateralisation phenotype in dogs shows substantial inter-individual variation, and that our sample size – similar to those used by Wells (2003) and by Quaranta et al. (2004) – was not sufficiently large to overcome sampling effects.

Despite these difficulties – in particular our failure to replicate the finding of Quaranta et al. (2004) – we conclude that the fact that we did find evidence in support of lateralisation of behaviour, and that there was a sex-difference in the same direction as reported by two previous studies suggests that dogs do indeed show a tendency towards lateralisation. Our findings give some indication as to why this lateralisation may exist. It seems probable that our two key findings of lateralisation and of a sex difference – in measures of first paw preference and of latency to first strike of the ball – are different ways of measuring the same phenotype. Because male dogs showed a shorter

latency to strike with the left paw, they displayed a tendency to use their left paw first when presented with the ball. Interestingly, the left-paw preference amongst males declined over sessions, which were carried out on different days, suggesting a long-term change in the dog's appreciation of the test, perhaps related to declining novelty.

This leads us to hypothesise that paw preference in dogs – and perhaps in other obligatory quadrupeds – is not a constant response, nor even a constant tendency, but a labile behaviour that changes with time. There is a precedent for our finding: examination of Fig. 2 in Quaranta et al. (2004) shows that male left paw preference in that study was substantially greater for the first paw used than for the whole 2-min testing period. Future studies of lateralised behaviour in dogs and other animals should take into account this possibility and analyse changes in response with time or familiarity with the test procedure.

This tendency for males to show left paw preference may be related to brain hemispheric specialisation in vertebrates. Similar findings have been reported in primates—lemurs (Ward et al., 1990), sifakas (Mason et al., 1995) and humans (Butler, 1984). In humans it is thought that increased exposure to peri- and prenatal testosterone in males results in a larger corpus callosum and increased left-handedness (Geschwind, 1984; Fitch et al., 1990). Three previous studies in non-primates have found evidence for a link between right hemispheric specialisation and behavioural laterality. Regolin and Vallortigara (1996) found that chicks tended to peck novel boxes more often when they were viewed with the left eye; while in zebrafish adults and larvae, the Left Eye System is preferentially involved in the assessment of novelty (Watkins et al., 2004). Finally, Tang and Verstynen (2002) reported a tendency for rats to use their left fore-paw when exposed to novel environments.

Together with the present study, these findings suggest an overall competence of the right hemisphere in responding to novelty. This view is widely held in studies of human behaviour (e.g. Goldberg and Costa, 1981) and the role of the right brain in responding to novelty may even produce asymmetric development of the hippocampus in the rat (Verstynen et al., 2001). The sex differences in the lateralisation of dog behaviour that have now been reported three times would imply that responses to novelty should differ in male and female dogs, including in measures that do not require a lateralised response from the animal. This prediction could be easily tested, and would open up two potential lines of investigation: the relation between lateralised behaviour and other behavioural phenotypes in dogs and other quadruped mammals, and the nature of sex differences in behaviour, in particular why males and females might show differences in their responses to novelty.

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