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Stability of motor bias in the domestic dog, *Canis familiaris*

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Running Headline: **Wells et al.:** Stability of paw use in dogs

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Abstract

This study explored the relationship between four measures of canine paw preference to establish whether the distribution, direction or strength of motor bias was consistent between tasks. Thirty-two dogs had their paw preferences tested using the *Kong ball, tape, lift paw* and *First-stepping* tests. A smaller sample were re-tested 6 months later. The distribution of the dogs' paw preferences was not significantly different from that expected by chance for the *Kong ball* and *lift paw* tests; dogs were significantly more inclined towards ambilaterality on the *tape* and *First-stepping* tests. More female dogs employed their right paw on the *lift paw* test; males were more likely to be ambilateral or left-pawed. There was no significant correlation in the direction of dogs' paw use for any tests. The *First-stepping* and *lift paw* tests were positively correlated for strength of paw use. Analysis revealed a significant correlation in direction and strength of dogs' paw use between the first and second attempts of all measures, except the *tape* test. Findings suggest that paw preference in the dog is not consistent between tasks, although stable over time. The study raises questions as to which test of paw preference is the most appropriate to employ.

Keywords: animal welfare, dogs, handedness, laterality, paw preferences

1. Introduction

Lateralised motor behaviour has been studied as an observable measure of cerebral functional asymmetry for numerous years (e.g., Harris, 1983; Springer and Deutsch, 1989). The most prominent manifestation of lateralised behaviour in humans is that of handedness (i.e., the predominant use of one hand), with roughly 90% of people using their right hand for most activities (Annett, 1985; Porac and Coren, 1981).

Studies now suggest that cerebral functional asymmetry is not unique to humans, but may be a fundamental feature of all vertebrate, and even some invertebrate, brains (for reviews see Frasnelli et al., 2012; MacNeilage et al., 2009; Rogers, 2002; Rogers et al., 2013; Vallortigara et al., 2010; Vallortigara and Rogers, 2005). What is less clear is whether non-human species exhibit lateralisation in their limb use in a manner that approximates human handedness or whether the preferred use of a specific hand, paw or similar appendage is related to other aspects of brain asymmetry (see reviews by Corballis, 2009; Rogers, 2009; Versace and Vallortigara, 2015). Whilst there is a general consensus that individual animals may show consistent hand/paw preferences, the question of whether motor lateralisation exists at the level of the population remains controversial (see MacNeilage et al., 1987). Population-level asymmetries have been found in a number of non-human species, including primates (e.g. Diamond and McGrew, 1994; Laska, 1996) and humpback whales (Clapham et al., 1995), but studies on other species, for example, sheep (e.g., Anderson and Murray, 2013; Morgante et al., 2010; Versace et al., 2007), horses (Austin and Rogers, 2012, 2014; Lucidi et al., 2013), cats (McDowell et al., 2016; Wells and Millsopp, 2009, 2012), and some insects (e.g., desert locust, Bell and Niven, 2014; tiger spider, Ades and Ramires, 2002), point more towards motor asymmetries at the level of the individual.

The domestic dog, *Canis familiaris*, has been shown to display lateral bias in the form of paw preferences at the level of the individual (e.g., McGreevy et al., 2010; Quaranta et al., 2004; Wells, 2003). Motor bias in this species has been tested using a variety of methods (for review see Siniscalchi et al., 2017), including reaching for food, removing something (e.g., adhesive tape, blanket) from the body, 'giving' a paw upon request, urinary posture and walking downstairs. Whilst a range of diverse measures have been employed to assess motor bias in the dog, investigations are largely united in only using one measure of paw preference per study. Only a handful of authors have compared dogs' paw use between tests, with mixed results. Wells (2003), for example, found strong positive correlations in the direction of dogs' paw use for two out of three (giving a paw, removing a blanket from the head, reaching for food) challenges. Tomkins and colleagues (2010), however, found no association in the distribution, direction or strength of dogs' paw preferences between the First-step and Kong ball tests. Poyser and colleagues (2006) similarly found no correlation in dogs' motor bias between tests including the paw used to hold a rawhide chew and that used to touch a food-laden ball. Establishing whether dogs harbour consistent paw preferences is important. It has been suggested that motor bias has the potential to be used as an applied tool for assessing vulnerability to stress and welfare risk in animals (see MacNeilage et al., 2009; Rogers, 2010). 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 and Caine, 2009; Cameron and Rogers, 1999). Left-sided biases of aggression, reactivity to fear-inducing stimuli and vigilance behaviour have also been noted in numerous species (e.g., Austin and Rogers, 2012; Denenberg, 1984; Koboroff et al., 2008; Lippolis et al., 2002, 2005; Zappia and Rogers, 1983). Thus, motor asymmetry has the potential to be used as a predictor of welfare risk. Recording accurate data on the direction and strength of an animal's motor bias is therefore important if the correct implications for welfare assessment are to be made.

99 Categorising an animal as ‘left-limbed’, for example, on the basis of its performance on one
100 paw preference test could provide misleading information on the emotional vulnerability of
101 that individual if paw preferences are task-specific and another test might lead to the same
102 animal being classified as ‘right-limbed’ or ambilateral.

103

104 The following study explores the relationship between four previously used measures of paw
105 preference in the domestic dog in an effort to establish whether the distribution, direction or
106 strength of motor bias is consistent or varies between tasks. A smaller sample of dogs are
107 tested again on the same challenges 6 months later to explore for test-retest reliability. The
108 study hopes to shed light on whether paw preference harbours any potential as an applied tool
109 for assessing vulnerability to stress or poor welfare in the dog and determine which test/s might
110 be the most appropriate to employ to this end.

111

2. Methods

2.1. Subjects

Thirty-two castrated pet dogs (18 males, 14 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. Animals ranged from 1 to 10 years of age (mean age=4.45, SEM±0.45years). 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 tests

Four previously employed tests were used to record the dogs' paw preferences:

2.2.1. Kong ball test

The Kong™ ball (KONG Company, Golden, CO, USA), a hollow, conical-shaped rubber toy that moves in an erratic manner, has been widely used to assess motor asymmetry in the domestic dog (Batt et al., 2007, 2008; Branson and Rogers, 2006; Marshall-Pescini et al., 2013; Plueckhahn et al., 2016; Schneider et al., 2013; Tomkins et al., 2010; Wells et al., 2016). A medium-sized Kong ball (10.5cm long) was used for testing. 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.

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.

2.2.2. Tape test

In line with previous studies (Batt et al., 2008; Quaranta et al., 2004), a 15mm X 50mm piece of adhesive tape (Scotch^{TM} tape, 3M, UK) was stuck to the dog's nose. The tape was adhered longitudinally to the midline dorsal surface of the animal's nose, with 75% of the tape hanging over the end of the dog's muzzle. Recording commenced as soon as the tape was adhered to the dog's nose. A paw use was classified as the animal using one of its paws to attempt to remove the tape. A separate paw use was considered to have been made when the animal removed its paw from its nose. Fifty individual paw uses (left plus right combined) were recorded for each animal.

2.2.3. Lift paw test

The dog was required, upon instruction from the Experimenter, to sit and lift its paw, i.e., 'give' a paw (see Wells, 2003). It was ensured that the animal was sitting symmetrically before the command to lift a paw was issued to prevent the possibility of unequal weight distribution between hind haunches influencing the dog's paw preference. The paw that was first lifted by the dog was recorded. The dog completed each paw lift in 5 blocks of 10, generating a total of 50 paw lifts per animal.

2.2.4. First-stepping test

In the First-stepping test, the first paw lifted by the dog in order to walk down a step was recorded on 50 occasions (see Tomkins et al., 2010). If a dog was too small for the standard step (height 0.18m; width 1.40m), i.e., the dog jumped down instead of stepping, smaller steps (height 0.05m; width 1.00m) were employed. Experimenter 1 stood on the upper level of the step next to the dog and held the animal loosely on a lead. Experimenter 2 stood on the base level, 2 metres away. When the dog was standing square with its forelegs level on the step, Experimenter 2 called the dog and recorded the paw lifted to step off. Both experimenters remained stationary while the dog stepped off. To give the dog a chance to rest, the task was completed over four sets of repetitions following the sequence 10-10-15-15. Each time, Experimenter 1 alternated her position by standing on the left or right hand-side of the dog.

2.3. Procedure

All of the dogs were required to undertake the 4 tests outlined above. To prevent over-tiring the subjects, the *Kong ball* and *tape* tests were both carried out in the dog's own home, while the *lift paw* and *First-stepping* tests were carried out on a separate day in the Animal Behaviour Centre, Queen's University Belfast. The order of testing was randomised between animals to control for potential order effects.

To explore for test-retest reliability in their expression of paw preference, a sample of available dogs (*Kong ball* n=20; *tape* n=16, *lift paw* n=10, *First-stepping* n=9) was tested again 6 months later on each of the measures. The procedure for the re-tests was exactly the same as outlined above (see 2.2.).

2.4. Analysis

A series of analyses were carried out to examine the distribution, direction and strength of the dogs' paw use across the tasks and to determine the stability of the dogs' paw preferences over time.

2.4.1. Distribution of paw use

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 on each of the four measures (*Kong ball* test, etc.). 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 preference and other variables, e.g., canine sex (McGreevy et al., 2010; Quaranta et al., 2004; Wells, 2003), a multinomial logistic regression was used to explore the effect of three possible predictor variables (canine sex [*male, female*]; age [*under 3 years; 4-6 years, >6 years*]; size [*small*, i.e., <21 inches in height, *large*, i.e., > 21 inches) on the dogs' paw preference classification (left, right, ambilateral). Statistical significances were established using the Likelihood ratio (χ^2) test. Any of the predictor variables found to be related to paw preference classification were used in further statistical models designed to explore the direction and strength of dogs' paw use.

212 *2.4.2. Direction of paw use*

213 A directional handedness index (HI) was calculated to quantify each dog's paw preference on
214 the four tests on a continuum from strongly left-paw preferent (+1) to strongly right paw-
215 preferent (-1). The HI was calculated by dividing the difference between the total number of
216 left and right paw reaches by their sum (L-R)/(L+R) [see Wells, 2003]. A one sample *t*-test
217 was conducted to explore for population-level laterality, comparing the dogs' HI scores to zero.
218 A mixed-design ANOVA was subsequently carried out to examine the effects of canine sex
219 (*male, female*) and test (*Kong ball, tape, lift paw, First-stepping*) on the direction of the dogs'
220 paw preferences.

221

222 *2.4.3. Strength of paw use*

223 The strength of the dogs' paw preferences was calculated for each task by taking the absolute
224 value of the HI scores (ABS-HI). A one sample *t*-test was conducted to explore for individual-
225 level laterality, comparing the dogs' absolute HI scores to zero. A mixed-design ANOVA was
226 also conducted to explore whether the strength of the dogs' paw preferences was influenced by
227 canine sex (*male, female*) or test (*Kong ball, tape, lift paw, First-stepping*).

228

229 *2.4.4. Stability of paw preference between tests and over time*

230 A series of Pearson product moment correlations were carried out to examine whether the
231 direction or strength of the dogs' paw preferences varied between the four tests, and, in the
232 smaller sample of dogs, between the first and second (6 months later) attempts at the tests.

233

234

235

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. Distribution of paw use

The distribution of the dogs' paw preferences was not significantly different from that expected by chance alone for the *Kong ball* (χ^2=0.81, df=2, p=0.67) and *lift paw* (χ^2=0.44, df=2, p=0.80) tests, although varied significantly for both the *tape* (χ^2=15.44, df=2, p<0.001) and *First-stepping* (χ^2=7.75, df=2, p=0.02) tests (Figures 1-2); dogs on both these tests were more inclined to be ambilateral than left- or right-pawed. Dogs were no more likely to be paw-preferent than ambilateral for any of the tests (p>0.05, binomial tests]. There was, likewise, no significant difference in the number of animals that were right- *vs.* left-paw preferent for any of the measures (p> 0.05, binomial tests).

(Figure 1 about here)

(Figure 2 about here)

Multinomial logistic regression was used to explore the effect of three predictor variables (canine age, sex, size) on paw preference classification (left, right, ambilateral) for each of the tests of motor bias. None of the predictor variables significantly (p>0.05) influenced the dogs' paw preferences on the *Kong ball*, *tape* or *First-stepping* tests. Canine sex, however, significantly predicted paw use on the *Lift paw* test (χ^2=7.23, df=2, p=0.02). More of the male dogs were classified as ambilateral or left-pawed on this task, while more of the female animals were right-pawed (Figure 3).

(Figure 3 about here)

3.2. Direction of paw use

The dogs' mean laterality scores did not differ significantly from zero for any of the tasks (one sample *t*-tests, $p>0.05$). The direction of the dogs' paw use did not differ significantly ($F[3,87]=0.15$, $p=0.93$) between the various tests of paw preference (Table 1). HI scores were not significantly influenced by canine sex ($F[1,29]=0.38$, $p=0.54$).

(Table 1 about here)

3.3. Strength of paw use

One sample t-tests showed that dogs' absolute strength of laterality scores differed significantly ($p<0.001$) from zero for all four tasks. The strength of the dogs' paw use also differed significantly between the tasks ($F[3,87]=7.19$, $p<0.001$). Post-hoc pairwise comparisons showed that dogs' paw preferences were significantly ($p<0.05$) stronger on the *lift paw* test than the *Kong ball, tape*, or *First-stepping*, tests (Table 1). The dogs' strength of paw use scores were also significantly ($P<0.05$) lower on the *tape* test than the *Kong ball* and *lift paw* tests. There was no significant effect of the dogs' sex on the strength of their motor bias ($F[1,29]=0.32$, $p=0.63$).

3.4. Correlation between tests of paw use

Analysis revealed no significant correlation between the HI scores for any of the measures employed to assess paw use ($p>0.05$ for all correlations). The strength of the dogs' paw preferences was not found to be significantly correlated for any of the measures except the *lift paw* and *First-stepping* tests, for which a positive correlation was unearthed ($r[33]=0.36$, $p=0.04$) [Figure 4].

(Figure 4 about here)

3.5. Test-retest reliability

Analysis revealed a significant positive correlation between the dogs' test and retest HI scores for the *Kong ball* ($r[20]=0.50$, $p=0.02$), *lift paw* ($r[10]=0.05$, $p=0.007$) and *First-stepping* ($r[9]=0.88$, $p=0.002$) tests. The dogs' HI scores were not significantly correlated between the first and second attempts on the *tape* test ($r[16]=0.05$, $p=0.85$).

There was a significant positive correlation between the test and retest ABS-HI scores for the *Kong ball* ($r[20]=0.65$, $p=0.02$), *lift paw* ($r[10]=0.97$, $p<0.001$) and *First-stepping* ($r[9]=0.87$, $p=0.002$) tests. There was no significant correlation between the original and retest absolute HI scores for the *tape* test ($r[16]=-0.20$, $p=0.45$).

4. Discussion

The findings from this study suggest that lateralised behaviour in the domestic dog is task-specific, but stable over time. The results raise questions as to the value of using certain measures of motor bias as an indicator of cerebral asymmetry in this species.

The results from this investigation point to a roughly equal distribution of lateralised (48%) and non-lateralised (52%) dogs across tasks. Existing research in this area is conflicting, with some studies highlighting a higher percentage of lateralised than non-lateralised animals (e.g., 75% lateralised [Tan, 1987]; 77% lateralised [Branson and 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 (*Kong ball* test-60% lateralised; *tape* test-34% lateralised; *lift paw*-60%; *First-stepping*-41% lateralised).

The direction of the dogs' paw use did not differ significantly from zero for any of the tests and analysis revealed no significant between-task correlations in the direction of the animals' paw use. The subjects recruited for this study were therefore not consistently left- or right-pawed, pointing to a lack of population-level laterality. Other studies in this area have, likewise, shown no significant correlation between various measures of paw use in dogs, e.g., Poyser et al., 2006; Tomkins et al., 2010; Batt et al., 2008). McGrew and Marchant (1997) have argued that true motor laterality reflects consistent limb use across all tasks. This is a trait

that some consider to be the typical difference between true human handedness and non-human task specialisation (McGrew and Marchant, 1994). The results from the current study, and other investigations on dogs (Tomkins et al., 2010; Wells, 2003), do not therefore support the interpretation of true 'pawedness' in the dog.

The dogs' strength of laterality scores differed significantly from zero for all four tasks, suggesting that individual dogs are lateralised with respect to their paw use, even though the direction of this preference is variable (see earlier). The strength of the dogs' paw preferences was found to be task-specific, although analysis revealed a significant positive correlation in strength of paw use between the *First-stepping* and *lift paw* tests. The dogs exhibited the strongest indication of lateral bias on the *lift paw* test, a finding that concurs with previous work in this area (Wells, 2003). This presents data contrary to the manipulation complexity hypothesis (Fagot and Vauclair, 1991), which suggests that more complex challenges should elicit stronger motor preferences than lower-level tasks that involve simple, routine actions. The *lift paw* exercise could certainly be considered a good example of a lower-level repetitive task, and one would therefore have expected a weaker lateral bias on this challenge. This particular exercise, however, contains a strong element of previous learning. Most owners teach their dog from an early stage to give a paw in exchange for a reward, e.g., food, verbal praise. Having learned that lifting a paw is reinforced, the chances of that same paw being used again are likely to be much higher. Whilst the dogs in the present study were not rewarded for their paw lifting during the task itself, the existing learned association may explain the stronger preference of dogs for one paw over the other on this particular task. Interestingly, this test also yielded a significant sex effect, with females being more inclined to use their right paw and males showing more of a tendency to ambilateral or left-paw use. Several studies have pointed to a relationship between paw preference and canine sex, with male animals

353 veering more towards left-paw use and females showing more of a tendency to use their right
354 paw (McGreevy et al., 2010; Quaranta et al., 2004; Wells, 2003). These studies, however, all
355 used non-castrated animals as subjects. Other investigations, either using castrated, or a
356 mixture of de-sexed and entire, animals have not reported a significant sex effect on dogs' paw
357 preferences (Batt et al., 2008; Branson and Rogers, 2006; Schneider et al., 2013; Wells et al.,
358 2017). It seems most likely that a hormonal factor is at play in explaining these disparate
359 results (see Geschwind and Galaburda, 1985a, 1985b; Witelson, 1991), although other,
360 potentially uncontrolled for, individual differences, warrant attention (see later).

361

362 Most of the tests employed in this study (with the exception of the *tape* test) demonstrated good
363 test-retest reliability. This confirms earlier work published on dogs' paw preferences (Batt et
364 al., 2008; Branson and Rogers, 2006), and, taken together, points to stability in canine paw
365 preference over time. However, the different tests of motor bias in this study yielded different
366 paw preferences in the same individual; this begs the question as to which one should be used.
367 Logistical factors may come into play when considering which test of laterality to employ.
368 Each paw preference task comes with its own unique set of advantages and disadvantages,
369 some of which will determine choice of test. For example, the *First-stepping* task has been
370 designed to remove the element of food motivation from paw preference testing and may
371 therefore be useful for animals that are not hungry enough to engage with the more food-
372 oriented *Kong ball* test. However, the *First-stepping* test is still an under-utilised measure and
373 the results from the current study present data contrary to those published by the innovators of
374 the test, who found more significant paw preferences with this tool (Tomkins et al., 2010). The
375 present investigation yielded a significant leaning towards ambilaterality on this test. Further
376 work is therefore needed to explore the utility of this test across contexts. The *Kong ball* test
377 is the most widely employed measure of canine paw preference. However, it is a time

consuming method of collecting paw preference data, in somecases taking several hours to complete. Moreover, Wells and colleagues (2016) have raised concerns with this test, drawing attention to the problems in assessing dominant paw use with this tool. Although not observed here, other authors have indicated that some dogs, notably smaller individuals, fail to engage with the Kong, giving rise to non-responses (Plueckhahn et al., 2016). The *tape* test raises several issues. The animals in this study were more inclined towards ambilateral than lateralised paw use on this test. Many of the dogs appeared stressed by the test (although physiological data would need to be collected to confirm this), making frantic paw movements aimed at removing the adhesive tape. Batt and colleagues (2007) noted a similar reaction in a group of dogs tested using the same approach. This particular test also presented logistical problems, including difficulties in getting the tape to adhere to the dogs' fur, particularly if the animals were long-haired. The dogs in this study also became increasingly wary of the Experimenter, showing avoidance at having the tape applied. Test-retest reliability was also found to be poor using this measure. For these reasons, the *tape* test is not considered a practical or desirable measure of paw preference in the dog. In many regards, the most useful test might be the *lift paw* exercise. The sex effect unearthed on this task points to a motor bias shaped by biological underpinnings.

The results from this study suggest that care needs to taken in classifying an individual dog as definitively ambilateral, left- or right-limbed, given the variability of paw use between tasks, a trait that is by no means unique to dogs (e.g., chimpanzees, Hopkins and Kimberly, 2000; marmosets, Hook and Rogers, 2008; capuchin monkeys, Truppa et al., 2016). Motor output will depend upon what type of cerebral processing is being used by an animal in any given situation and will be shaped by a wide variety of extrinsic and intrinsic factors. For example, the demands of the task will have a role to play. Studies on species including primates and

403 chicks (for reviews see Rogers, 2009; Versace and Vallortigara, 2015) have shown that
404 temporal sequencing and non-spatial tasks result in more dominant left hemisphere processing
405 and a subsequent leaning towards right limb motor use, while spatial exercises and tasks
406 demanding attention to a novel stimulus encourage predominately right hemisphere processing
407 and left limb output. Individual differences will also interact with task demands in determining
408 the degree to which one or both hemispheres are employed to process information and
409 behavioural lateralisation. Laterality has been linked to personality in some species (e.g., fish
410 - Brown and Bibost, 2014; cats - McDowell et al., 2016), including, more recently, dogs
411 (Barnard et al., 2017), with authors finding a strong relationship between traits associated with
412 stronger emotional reactivity (aggressiveness, fearfulness, sociability) and ambilaterality. In a
413 similar vein, Branson and Rogers (2010) found that mixed paw use on the Kong test is
414 associated with an increased fear of thunderstorm sounds in dogs, highlighting the association
415 between emotional functioning and motor output. The affective state of the individual and
416 their cognitive bias may also influence motor output, and may go some part to explaining the
417 lack of correlation in paw use between tasks in the present study. Gordon and Rogers (2015)
418 found that marmosets that exhibited a negative cognitive bias were more likely to be left-
419 handed. More recently, Wells and others (2017) found that left-pawed dogs were more
420 negative or "pessimistic" in their cognitive outlook than right-pawed or ambilateral individuals.
421 Further work is clearly needed to examine the complex relationship between limb use and
422 individual differences, largely to determine whether these are variables that need to be
423 controlled for in future studies.

424

425 Overall, the results from this study suggest that paw preference in the domestic dog is not
426 consistent between tasks, although is largely stable over time, regardless of how it is assessed.
427 Several authors have drawn attention to the purported association between motor bias and

428 animal welfare (Barnard et al., 2017; Rogers 2010; Wells et al., 2017), but the findings from
429 this, and other recent studies, raise questions as to which test of paw preference may be the
430 most appropriate to employ to this end. Further work is needed to explore the complex
431 relationship between limb use and brain lateralisation before firm conclusions on the merits of
432 using paw preference as a tool for assessing at-risk individuals can be drawn. In the meantime,
433 the use of multiple measures of well-being (e.g., heart-rate, cortisol, behaviour), in addition to
434 paw use, is recommended in the assessment of animal welfare.

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580 Table Legend

581

582 Table 1. Mean HI and ABS-Hi scores for 4 tests of motor bias

583 Figure Legends

584

585 Figure 1. The percentage of dogs classified as ambilateral, right- and left-pawed on 4 tests of
586 motor bias

587

588 Figure 2. Frequency distribution of dogs' HI scores from +1 to -1 (presented in units of 0.01)

589

590 Figure 3. Frequency distribution of male and female dogs' HI scores on the *lift paw* test
591 (scores presented in units of 0.01)

592

593 Figure 4. Scattergram showing the relationship between the dogs' ABS-HI (strength of paw
594 use) scores on the *lift paw* and *First-stepping* tests

595 Table 1.

Test of laterality	**Mean (+/-se) HI**	**Mean (+/-se) ABS-HI**
Kong ball	-0.02 (0.07)	0.31 (0.04)
Tape	0.03 (0.04)	0.20 (0.03)
Lift paw	0.02 (0.10)	0.46 (0.06)
First stepping	-0.04 (0.06)	0.28 (0.04)

596

Figure 1.

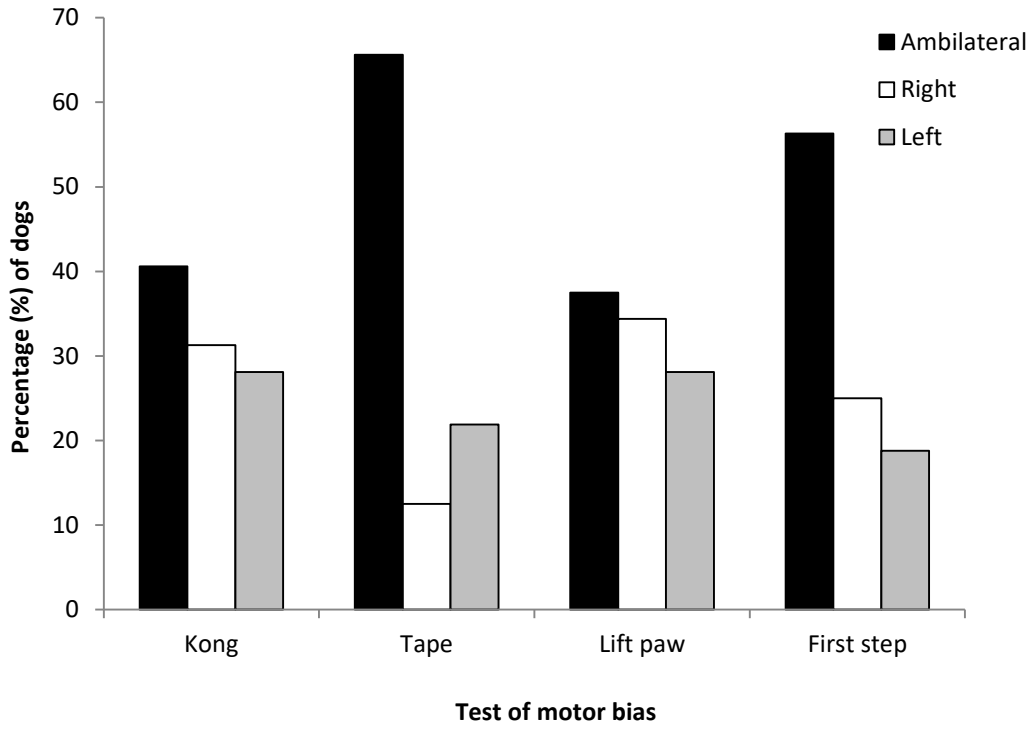

70
60
50
40
30
20
10
0
Percentage (%) of dogs
Ambilateral
Right
Left
Kong
Tape
Lift paw
First step
Test of motor bias

Figure 2.

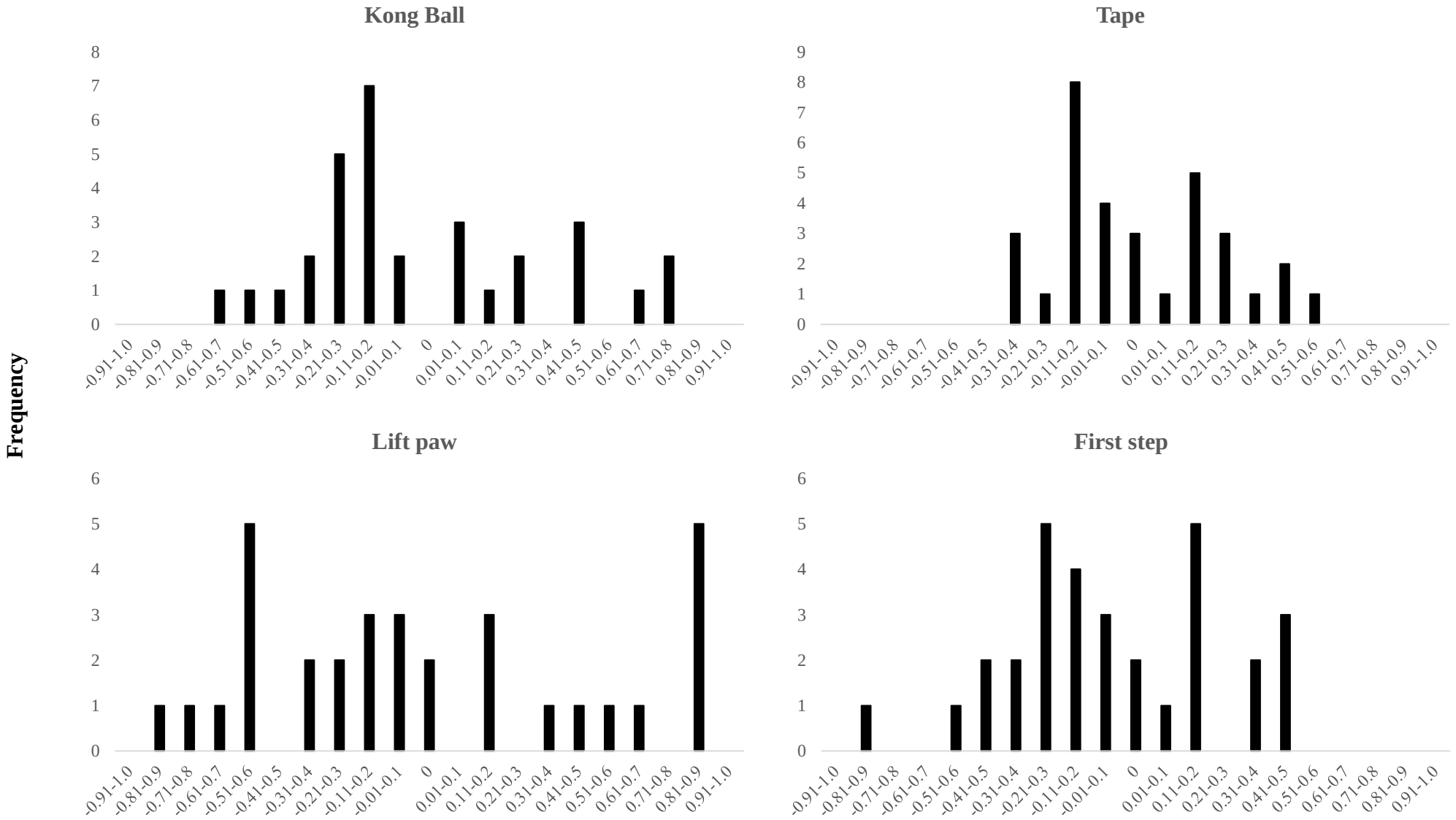

Kong Ball
Tape
Lift paw
First step
Frequency
-0.91-1.0
-0.81-0.9
-0.71-0.8
-0.61-0.7
-0.51-0.6
-0.41-0.5
-0.31-0.4
-0.21-0.3
-0.11-0.2
-0.01-0.1
0
0.01-0.1
0.11-0.2
0.21-0.3
0.31-0.4
0.41-0.5
0.51-0.6
0.61-0.7
0.71-0.8
0.81-0.9
0.91-1.0

Figure 3.

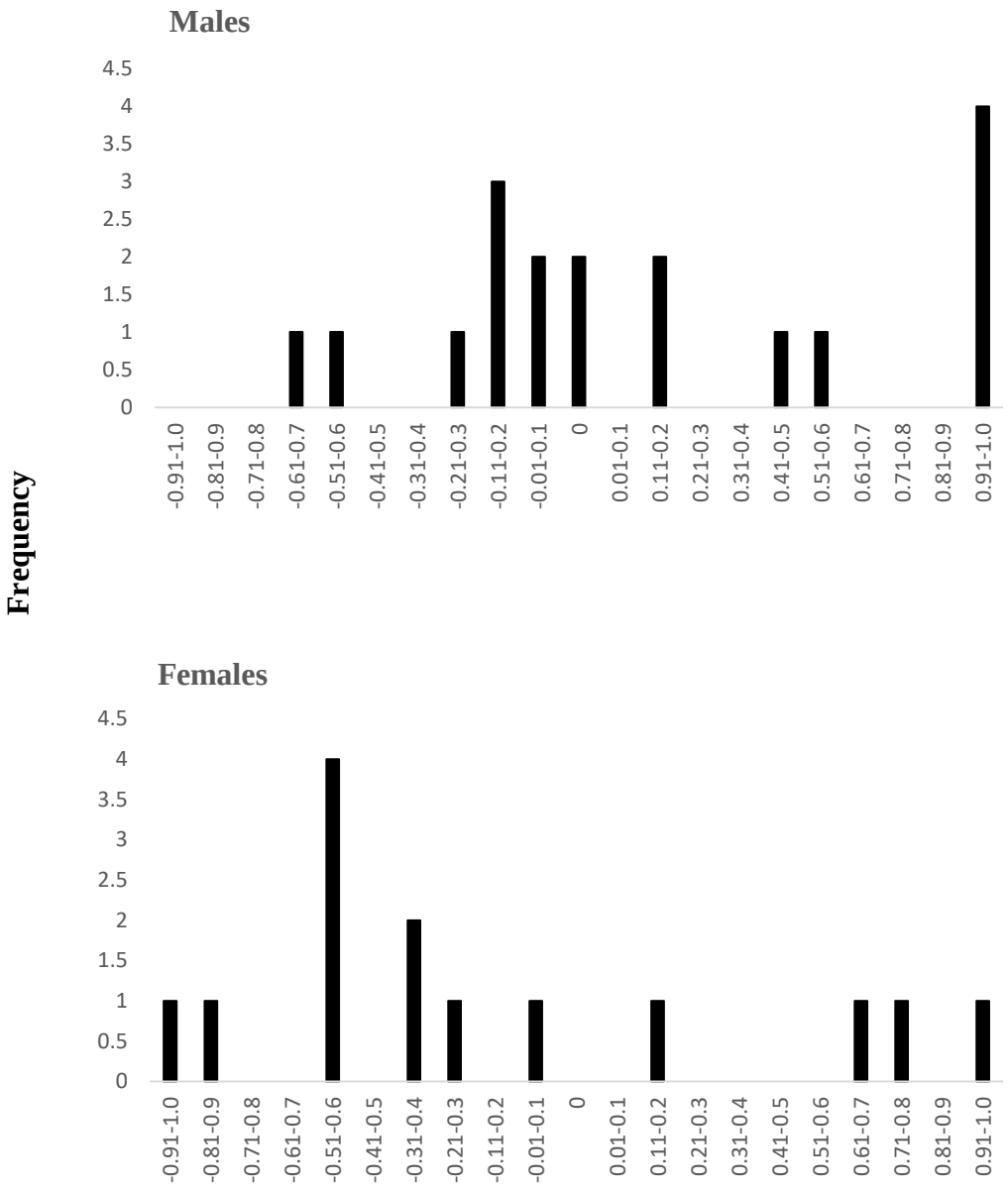
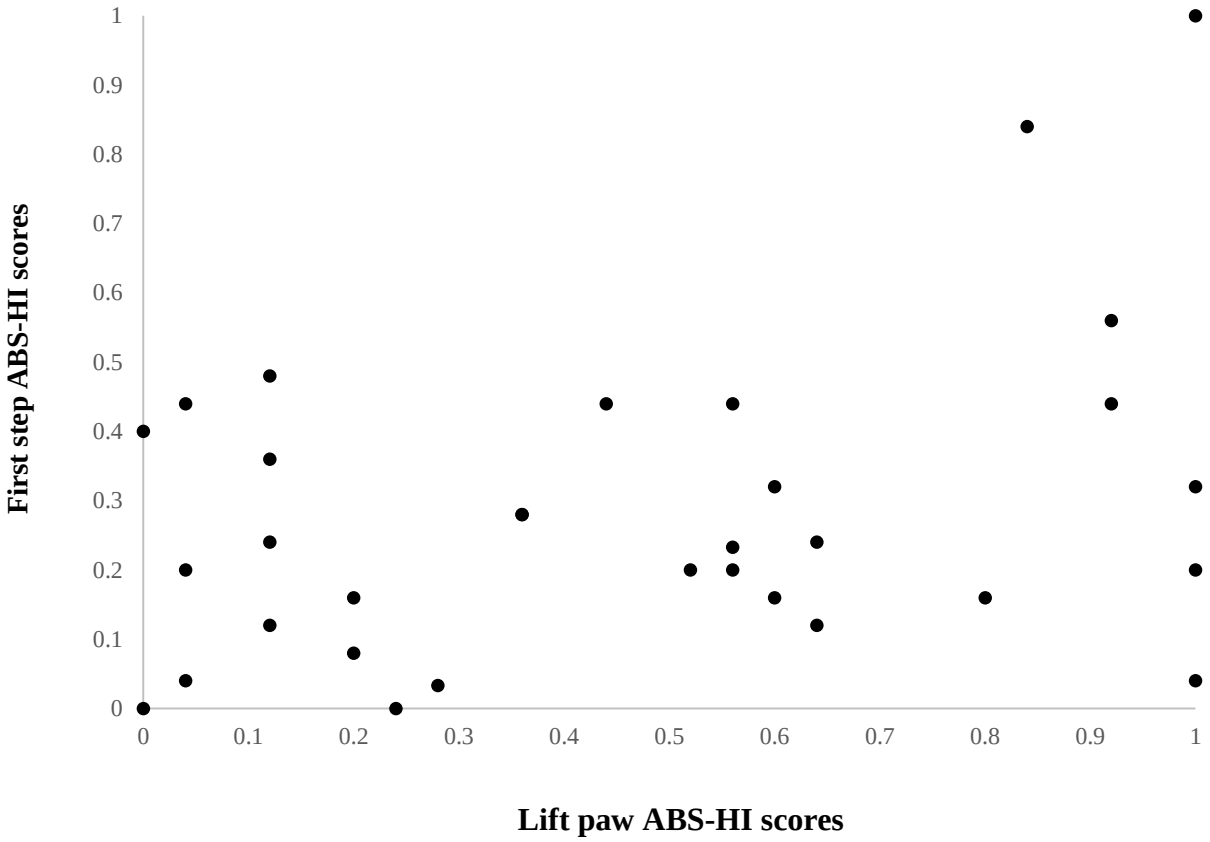

Males
Frequency
4.5
4
3.5
3
2.5
2
1.5
1
0.5
0
-0.91-1.0
-0.81-0.9
-0.71-0.8
-0.61-0.7
-0.51-0.6
-0.41-0.5
-0.31-0.4
-0.21-0.3
-0.11-0.2
-0.01-0.1
0
0.01-0.1
0.11-0.2
0.21-0.3
0.31-0.4
0.41-0.5
0.51-0.6
0.61-0.7
0.71-0.8
0.81-0.9
0.91-1.0
Females

Figure 4.


First step ABS-HI scores
Lift paw ABS-HI scores
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1