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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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26 **Abstract**

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

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

48

49 **1. Introduction**

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

55

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

73

74 The domestic dog, *Canis familiaris*, has been shown to display lateral bias in the form of paw
75 preferences at the level of the individual (e.g., McGreevy et al., 2010; Quaranta et al., 2004;
76 Wells, 2003). Motor bias in this species has been tested using a variety of methods (for review
77 see Siniscalchi et al., 2017), including reaching for food, removing something (e.g., adhesive
78 tape, blanket) from the body, ‘giving’ a paw upon request, urinary posture and walking
79 downstairs. Whilst a range of diverse measures have been employed to assess motor bias in
80 the dog, investigations are largely united in only using one measure of paw preference per
81 study. Only a handful of authors have compared dogs’ paw use between tests, with mixed
82 results. Wells (2003), for example, found strong positive correlations in the direction of dogs’
83 paw use for two out of three (giving a paw, removing a blanket from the head, reaching for
84 food) challenges. Tomkins and colleagues (2010), however, found no association in the
85 distribution, direction or strength of dogs’ paw preferences between the First-step and Kong
86 ball tests. Poyser and colleagues (2006) similarly found no correlation in dogs’ motor bias
87 between tests including the paw used to hold a rawhide chew and that used to touch a food-
88 laden ball. Establishing whether dogs harbour consistent paw preferences is important. It has
89 been suggested that motor bias has the potential to be used as an applied tool for assessing
90 vulnerability to stress and welfare risk in animals (see MacNeilage et al., 2009; Rogers, 2010).
91 Left-limbed animals, which tend to be right-hemisphere dominant, show stronger fear
92 responses than right-limbed animals, which tend to be left-hemisphere dominant (e.g., Braccini
93 and Caine, 2009; Cameron and Rogers, 1999). Left-sided biases of aggression, reactivity to
94 fear-inducing stimuli and vigilance behaviour have also been noted in numerous species (e.g.,
95 Austin and Rogers, 2012; Denenberg, 1984; Koboroff et al., 2008; Lippolis et al., 2002, 2005;
96 Zappia and Rogers, 1983). Thus, motor asymmetry has the potential to be used as a predictor
97 of welfare risk. Recording accurate data on the direction and strength of an animal’s motor
98 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

112 **2. Methods**

113

114 *2.1. Subjects*

115 Thirty-two castrated pet dogs (18 males, 14 females) of mixed breed were recruited via
116 response to an email advertising a study on paw preferences sent to pet owners in Northern
117 Ireland, UK. Animals ranged from 1 to 10 years of age (mean age=4.45, SEM±0.45years).
118 All of the dogs were family pets living in households and whose owners had consented to them
119 taking part in the study. None of the dogs had undergone any behavioural training, nor had
120 any disability preventing them from completing the study.

121

122 *2.2. Paw preference tests*

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

124

125 *2.2.1. Kong ball test*

126 The Kong™ ball (KONG Company, Golden, CO, USA), a hollow, conical-shaped rubber toy
127 that moves in an erratic manner, has been widely used to assess motor asymmetry in the
128 domestic dog (Batt et al., 2007, 2008; Branson and Rogers, 2006; Marshall-Pescini et al., 2013;
129 Plueckhahn et al., 2016; Schneider et al., 2013; Tomkins et al., 2010; Wells et al., 2016). A
130 medium-sized Kong ball (10.5cm long) was used for testing. The ball has a 2.9cm diameter
131 hole at one end, and a smaller 1cm diameter hole at the opposite end. Before testing, the toy
132 was filled through the larger hole with moist dog food (Pedigree™, original flavour, Waltham
133 Mars, UK) and frozen. Balls were washed thoroughly in-between tests.

134

135 At the start of testing, the dog was shown, and allowed to sniff, the food-loaded Kong ball. The
136 toy was then placed directly in front of the animal. The paw used to stabilise the Kong by the

137 dog was recorded by the Experimenter. A paw use was classified as the animal having one or
138 both paws on the Kong ball, regardless of duration. A separate paw use was considered to have
139 been made when the animal removed its paw from the Kong and replaced one or both of its
140 paws on the object. On occasion, dogs used both paws to stabilise the ball; these occurrences
141 were recorded, but testing was not considered complete until one hundred paw uses (left plus
142 right combined) had been made by the animal, regardless of the number of times dogs
143 employed both paws.

144

145 *2.2.2. Tape test*

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

154

155 *2.2.3. Lift paw test*

156 The dog was required, upon instruction from the Experimenter, to sit and lift its paw, i.e., 'give'
157 a paw (see Wells, 2003). It was ensured that the animal was sitting symmetrically before the
158 command to lift a paw was issued to prevent the possibility of unequal weight distribution
159 between hind haunches influencing the dog's paw preference. The paw that was first lifted by
160 the dog was recorded. The dog completed each paw lift in 5 blocks of 10, generating a total of
161 50 paw lifts per animal.

162 2.2.4. *First-stepping test*

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

173

174 2.3. *Procedure*

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

180

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

185

186 2.4. *Analysis*

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

190

191 *2.4.1. Distribution of paw use*

192 Binomial z -scores were calculated to determine whether the frequency of right- or left-paw use
193 exceeded that expected by chance. An alpha value of 0.05 was adopted for all analyses. A z -
194 score greater than +1.96 (two-tailed) reflected a significant left paw preference, whilst a z -score
195 less than -1.96 indicated a significant right paw preference. Dogs with z -scores between +1.96
196 and -1.96 were classified as ambilateral.

197

198 A one-way chi-squared analysis was carried out to investigate whether there was a significant
199 difference in the distribution of the dogs' paw preferences on each of the four measures (*Kong*
200 *ball* test, etc.). Binomial tests were also conducted to determine whether there was a significant
201 difference in the number of animals that were: (1) paw-preferent (either to the left or right) *vs.*
202 ambilateral, and; (2) right- *vs.* left-paw preferent. Given the reported link between paw
203 preference and other variables, e.g., canine sex (McGreevy et al., 2010; Quaranta et al., 2004;
204 Wells, 2003), a multinomial logistic regression was used to explore the effect of three possible
205 predictor variables (canine sex [*male, female*]; age [*under 3 years; 4-6 years, >6 years*]; size
206 [*small, i.e., <21 inches in height, large, i.e., > 21 inches*]) on the dogs' paw preference
207 classification (left, right, ambilateral). Statistical significances were established using the
208 Likelihood ratio (χ^2) test. Any of the predictor variables found to be related to paw preference
209 classification were used in further statistical models designed to explore the direction and
210 strength of dogs' paw use.

211

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

236 **Ethical approval**

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

241 **3. Results**

242

243 *3.1. Distribution of paw use*

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

252

253 (Figure 1 about here)

254 (Figure 2 about here)

255

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

263

264 (Figure 3 about here)

265

266 3.2. *Direction of paw use*

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

271

272 (Table 1 about here)

273

274 3.3. *Strength of paw use*

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

283

284 3.4. *Correlation between tests of paw use*

285 Analysis revealed no significant correlation between the HI scores for any of the measures
286 employed to assess paw use ($p>0.05$ for all correlations). The strength of the dogs' paw
287 preferences was not found to be significantly correlated for any of the measures except the *lift*
288 *paw* and *First-stepping* tests, for which a positive correlation was unearthed ($r[33]=0.36$,
289 $p=0.04$) [Figure 4].

290

291 (Figure 4 about here)

292

293 3.5. Test-retest reliability

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

298

299 There was a significant positive correlation between the test and retest ABS-HI scores for the
300 *Kong ball* ($r[20]=0.65$, $p=0.02$), *lift paw* ($r[10]=0.97$, $p<0.001$) and *First-stepping* ($r[9]=0.87$,
301 $p=0.002$) tests. There was no significant correlation between the original and retest absolute
302 HI scores for the *tape* test ($r[16]=-0.20$, $p=0.45$).

303

304

305 4. Discussion

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

309

310 The results from this investigation point to a roughly equal distribution of lateralised (48%)
311 and non-lateralised (52%) dogs across tasks. Existing research in this area is conflicting, with
312 some studies highlighting a higher percentage of lateralised than non-lateralised animals (e.g.,
313 75% lateralised [Tan, 1987]; 77% lateralised [Branson and Rogers, 2006]; 79% lateralised
314 [Siniscalchi et al., 2008]), and others showing more of an equal distribution of ambilateral and
315 paw-preferent individuals (46% lateralised [Marshall-Pescini et al., 2013]; 37% lateralised
316 [McGreevy et al., 2010]; 52% lateralised [Tomkins et al., 2010]). The results from the present
317 investigation add to the conflict, but are more in line with those studies pointing to a roughly
318 equal split of lateralised and non-lateralised dogs (*Kong ball* test-60% lateralised; *tape* test-
319 34% lateralised; *lift paw*-60%; *First-stepping*-41% lateralised).

320

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

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

332

333 The dogs’ strength of laterality scores differed significantly from zero for all four tasks,
334 suggesting that individual dogs are lateralised with respect to their paw use, even though the
335 direction of this preference is variable (see earlier). The strength of the dogs’ paw preferences
336 was found to be task-specific, although analysis revealed a significant positive correlation in
337 strength of paw use between the *First-stepping* and *lift paw* tests. The dogs exhibited the
338 strongest indication of lateral bias on the *lift paw* test, a finding that concurs with previous work
339 in this area (Wells, 2003). This presents data contrary to the manipulation complexity
340 hypothesis (Fagot and Vauclair, 1991), which suggests that more complex challenges should
341 elicit stronger motor preferences than lower-level tasks that involve simple, routine actions.
342 The *lift paw* exercise could certainly be considered a good example of a lower-level repetitive
343 task, and one would therefore have expected a weaker lateral bias on this challenge. This
344 particular exercise, however, contains a strong element of previous learning. Most owners
345 teach their dog from an early stage to give a paw in exchange for a reward, e.g., food, verbal
346 praise. Having learned that lifting a paw is reinforced, the chances of that same paw being
347 used again are likely to be much higher. Whilst the dogs in the present study were not rewarded
348 for their paw lifting during the task itself, the existing learned association may explain the
349 stronger preference of dogs for one paw over the other on this particular task. Interestingly,
350 this test also yielded a significant sex effect, with females being more inclined to use their right
351 paw and males showing more of a tendency to ambilateral or left-paw use. Several studies
352 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

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

395

396 The results from this study suggest that care needs to taken in classifying an individual dog as
397 definitively ambilateral, left- or right-limbed, given the variability of paw use between tasks, a
398 trait that is by no means unique to dogs (e.g., chimpanzees, Hopkins and Kimberly, 2000;
399 marmosets, Hook and Rogers, 2008; capuchin monkeys, Truppa et al., 2016). Motor output
400 will depend upon what type of cerebral processing is being used by an animal in any given
401 situation and will be shaped by a wide variety of extrinsic and intrinsic factors. For example,
402 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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438 **References**

- 439 Ades, C., Ramires, E.N., 2002. Asymmetry of leg use during prey handling in the spider
440 *Scytodes globula* (Scytodidae). *J. Insect Behav.* 15, 563-570.
- 441 Anderson, D.M., Murray, L.W., 2013. Sheep laterality. *Laterality* 18, 179-193.
- 442 Annett, M., 1985. *Left, Right, Hand and Brain: the Right Shift Theory*. Lawrence Erlbaum,
443 New York.
- 444 Association for the Study of Animal Behaviour, 2006. Guidelines for the treatment of animals
445 in behavioural research and teaching. *Anim. Behav.* 71, 245-253.
- 446 Austin, N.P., Rogers, L.J., 2012. Limb preferences and lateralization of aggression, reactivity
447 and vigilance in feral horses, *Equus caballus*. *Anim. Behav.* 83, 239-247.
- 448 Austin, N.P., Rogers, L.J., 2014. Lateralization and agonistic and vigilance responses in
449 Prewalski horses (*Equus przewalskii*). *Appl. Anim. Behav. Sci.* 151, 43-50.
- 450 Barnard S., Wells, D.L., Hepper P.G., Milligan A.D.S., 2017. Association between lateral bias
451 and personality traits in the domestic dog. *J. Comp. Psychol.* 131, 246-256.
- 452 Batt, L.S., Batt, M.S., Baguley, J.A., McGreevy, P.D., 2008. Factors associated with success
453 in guide dog training. *J. Vet. Beh.* 3, 143-151.
- 454 Batt, L., Batt, M., McGreevy, P., 2007. Two tests for motor laterality in dogs. *J. Vet. Behav.*
455 2, 47-51.
- 456 Bell, A.T.A., Niven, J.E., 2014. Individual-level, context-dependent handedness in the desert
457 locust. *Current Biol.* 24, R382-383.
- 458 Braccini, S.N., Caine, N.G., 2009. Hand preference predicts reactions to novel foods and
459 predators in Marmosets (*Callithrix geoffroyi*). *J. Comp. Psychol.* 123, 18-25.
- 460 Branson, N.J., Rogers, L.J., 2006. Relationship between paw preference strength and noise
461 phobia in *Canis familiaris*. *J. Comp. Psychol.* 120, 176-183.

462 Brown, C., Bibost, A., 2014. Laterality is linked to personality in the black-lined rainbowfish,
463 *Melanotaenia nigrans*. Behav. Ecol. Sociobiol. 68, 999-1005.

464 Cameron, R., Rogers, L.J., 1999. Hand preference of the common marmoset (*Callithrix*
465 *jacchus*): problem solving and responses in a novel setting. J. Comp. Psychol. 113, 149-
466 157.

467 Clapham, P.J., Leimkuhler, E., Gray, B.K., Mattila, D.K., 1995. Do humpback whales exhibit
468 lateralized behaviour? Anim. Behav. 50, 73-82.

469 Corballis, M.C., 2009. The evolution and genetics of cerebral asymmetry. Phil. Trans. Roy.
470 Soc. B 364, 867-879.

471 Denenberg, V.H., 1984. Effects of right hemisphere lesions in rats. In: Ardilla, A, Ostosky-
472 Solis, P. (Eds), Right Hemisphere: Neurology and Neuropsychology. Gordon & Breach,
473 New York, pp. 241-264.

474 Diamond, A.C., McGrew, W.C., 1994. True handedness in the cotton-top tamarin (*Saguinus*
475 *oedipus*). Primates 35, 69-77.

476 Fagot, J., Vauclair, J., 1991. Manual laterality in nonhuman primates: A distinction between
477 handedness and manual specialization. Psychol. Bull. 109, 76-89.

478 Frasnelli, E., Vallortigara, G., Rogers L.J. 2012. Left-right asymmetries of behaviour and
479 nervous system in invertebrates. Neurosci. Biobehav. Review 36, 1273–1291.

480 Geschwind, N., Galaburda, A.M., 1985a. Cerebral lateralization: biological mechanisms,
481 associations, and pathology: II. A hypothesis and a program for research. Neurol Archive 42,
482 521-552.

483 Geschwind, N., Galaburda, A.M., 1985b. Cerebral lateralization: biological mechanisms,
484 associations, and pathology: III. A hypothesis and a program for research. Neurol Archive
485 42, 634-654.

486 Gordon, D.J., Rogers, L.J., 2015. Cognitive bias, hand preference and welfare of common
487 marmosets. *Behav. Brain Res.* 287, 100-108.

488

489 Harris, L.J., 1983. Laterality of function in the infant: Historical and contemporary trends in
490 theory and research. In: Young, G., Segalowitz, S.J., Corter, C.M., Trehub, S.E. (Eds.),
491 *Manual Specialization and the Developing Brain*. Academic Press, New York, pp. 177-247.

492 Hook, M.A., Rogers, L.J., 2008. Visuospatial reaching preferences of common marmosets
493 (*Callithrix jacchus*): An assessment of individual biases across a variety of tasks. *J. Comp.*
494 *Psychol.* 122, 41-51.

495 Hopkins, W.D., Kimberly, P., 2000. Chimpanzee (*Pan troglodytes*) handedness: variability
496 across multiple measures of hand use. *J. Comp. Psych.* 114, 126-135.

497 Koboroff, A., Kaplan, G., Rogers, L.J., 2008. Hemispheric specialization in Australian
498 magpies (*Gymnorhina tibicen*) shown as eye preferences during response to a predator.
499 *Brain Res. Bull.* 76, 304-306.

500 Laska, M., 1996. Manual laterality in spider monkeys (*Ateles geoffroyi*) solving visually and
501 tactually guided food-reaching tasks. *Cortex* 32, 717-726.

502 Lippolis, G., Bisazza, A., Rogers, L.J., Vallortigara, G., 2002. Lateralisation of predator
503 avoidance responses in three species of toads. *Laterality* 7, 163-183.

504 Lippolis, G., Westman, W., McAllan, B.M., Rogers, L.J., 2005. Lateralisation of escape
505 responses in the stripe-faced dunnart, *Sminthopsis macroura*. *Laterality* 10, 457-470.

506 Lucidi, P., Bacco, G., Sticco, M. et al., 2013. Assessment of motor laterality in foals and young
507 horses (*Equus caballus*) through an analysis of derailment at trot. *Physiol. Behav.* 109, 8-
508 13.

509 MacNeilage, P.F., Rogers, L.J., Vallortigara, G. 2009. Origins of the left and right brain. *Sci.*
510 *Am.* 301, 60-67.

511 MacNeilage, P.F., Studdert-Kennedy, M.G., Lindblom, B., 1987. Primate handedness
512 reconsidered. *Behav. Brain Sci.* 10, 247-263.

513 Marshall-Pescini, S., Barnard, S., Branson, N.J., Valsecchi, P., 2013. The effect of preferential
514 paw usage on dogs' (*Canis familiaris*) performance in a manipulative problem-solving task.
515 *Behav. Proc.* 100, 40-43.

516 McDowell, L.J., Wells, D.L., Hepper, P.G., Dempster, M. 2016. Lateral bias and temperament
517 in the domestic cat, *Felis silvestris*. *J. Comp. Psychol.* 130, 313-320.

518 McGreevy, P.D., Brueckner, A., Thomson, P.C., & Branson, N.J. , 2010. Motor laterality in 4
519 breeds of dogs. *J. Vet. Behav.* 5, 318-323.

520 McGrew, W.C., Marchant, L.F., 1997. On the other hand: Current issues in and meta-analysis
521 of the behavioral laterality of hand function in nonhuman primates. *Yearbook of Physical*
522 *Anthropol.* 40, 201-232.

523 McGrew, W.C., Marchant, L.F., 1994. Primate ethology: a perspective on human and
524 nonhuman handedness. In: Bock, P.K. (Ed.), *Handbook of Psychological Anthropology*
525 Greenwood Press, Westport, pp 171-184.

526 Morgante, M., Giancesella, M., Versace, E., et al., 2010. Preliminary study on metabolic profile
527 of pregnant and non-pregnant ewes with high or low degree of behavioural lateralization.
528 *Anim. Sci. J.* 81, 722-730.

529 Plueckhahn, T., Schneider, L.A., Delfrabbo, P.H., 2016. Assessing lateralization in domestic
530 dogs: performance by *Canis familiaris* on the Kong test. *J. Vet. Beh.* 15, 25-30.

531 Porac, C., Coren, S., 1981. *Lateral Preferences and Human Behavior*. Springer-Verlag,
532 New York.

533 Poyser, G., Caldwell, C., Cobb, M., 2006. Dog paw preference shows lability and sex
534 differences. *Behav. Proc.* 73, 216-221.

535 Quaranta, A., Siniscalchi, M., Frate, A., Vallortigara, G., 2004. Paw preference in dogs:
536 relations between lateralised behaviour and immunity. *Behav. Brain Res.* 153, 521-525.

537 Rogers, L.J., 2002. Lateralization in vertebrates: Its early evolution, general pattern, and
538 development. *Adv. Study Behav.* 31, 107-161.

539 Rogers, L.J., 2009. Hand and paw preferences in relation to the lateralized brain. *Phil. Trans.*
540 *Roy. Soc. B* 364, 943-954.

541 Rogers, L.J. 2010. Relevance of brain and behavioural lateralization to animal welfare. *Appl.*
542 *Anim. Behav. Sci.* 127, 1-11.

543 Rogers L.J., Vallortigara., G., Andrew R.J. 2013. Divided brains: The biology and behaviour
544 of brain asymmetries. Cambridge University Press, Cambridge.

545 Schneider, L.A., Delfabbro, P.H., Burns, N.R., 2013. Temperament and lateralization in the
546 domestic dog (*Canis familiaris*). *J. Vet. Behav.* 8, 124-134.

547 Siniscalchi, M., d'Ingeo, S., Quaranta, A. 2017. Lateralized functions in the dog brain.
548 *Symmetry* 9, 71.

549 Siniscalchi, M., Quaranta, A., Rogers, L.J. 2008. Hemispheric specialisation in dogs for
550 processing different acoustic stimuli. *PloS One*, 3, e3349.

551 Springer, S.P., Deutsch, G., 1989. *Left Brain, Right Brain*. W.H. Freeman, New York.

552 Tan, U., 1987. Paw preferences in dogs. *Int. J. Neuroscience* 32, 825-829.

553 Tomkins, L.M., Thomson, P.C., McGreevy, P.D., 2010. First-stepping Test as a measure of
554 motor laterality in dogs (*Canis familiaris*). *J. Vet. Behav.* 5, 247-255.

555 Truppa, V., Spinozzi, G., Lagana, T., Mortari, E. P., Sabbatini, G., 2016. Versatile grasping
556 ability in power-grip actions by tufted capuchin monkeys (*Sapajus* spp.). *Am. J. Phys.*
557 *Anthropol.* 159, 63-72.

558 Vallortigara, G., Chiandetti, C., Sovrano, V.A. 2010. Brain asymmetry (animal). *WIREs Cog.*
559 *Sci.* DOI: 10.1002/WCS.100.

560 Vallortigara, G., Rogers, L.J. 2005. Survival with an asymmetrical brain: Advantages and
561 disadvantages of cerebral lateralization. *Behav. Brain Sci.* 28, 575-633.

562 Versace, E., Morgante, M., Pulina, G., Vallortigara, G., 2007. Behavioural lateralization in
563 sheep (*Ovis aries*). *Behav. Brain Res.* 184, 72-80.

564 Versace, E., Vallortigara, G. 2015. Forelimb preferences in human beings and other species:
565 multiple models for testing hypotheses on lateralization. *Front. Psychol.* 6, 1-9.

566 Wells, D.L., 2003. Lateralised behaviour in the domestic dog, *Canis familiaris*. *Behav. Proc.*
567 61, 27-35.

568 Wells, D.L., Hepper, P.G., Milligan, A.D.S., Barnard, S. 2016. Comparing lateral bias in dogs
569 and humans using the Kong™ ball test. *Appl. Anim. Behav. Sci.* 176, 70-76.

570 Wells, D.L., Hepper, P.G., Milligan, A.D.S. & Barnard, S., 2017. Cognitive bias and paw
571 preference in the domestic dog, *Canis familiaris*. *J. Comp. Psychol.* 131, 317-325.

572 Wells, D.L., Millsopp, S., 2009. Lateralised behaviour in the domestic cat, *Felis silvestris*
573 *catus*. *Anim. Behav.* 78, 537-541.

574 Wells, D.L., Millsopp, S., 2012. The ontogeny of lateralised behaviour in the domestic cat,
575 *Felis silvestris catus*. *J. Comp. Psychol.* 126, 23-30.

576 Witelson, S.F. 1991. Neural sexual mosaicism: Sexual differentiation of the human temporo-
577 parietal region for functional asymmetry. *Psychoneuroendocrinology* 16, 131-153.

578 Zappia, J.V., Rogers, L.J., 1983. Light experience during development affects asymmetry of
579 forebrain function in chickens. *Dev. Brain Res.* 11, 93-106.

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
<i>Kong ball</i>	-0.02 (0.07)	0.31 (0.04)
<i>Tape</i>	0.03 (0.04)	0.20 (0.03)
<i>Lift paw</i>	0.02 (0.10)	0.46 (0.06)
<i>First stepping</i>	-0.04 (0.06)	0.28 (0.04)

596

Figure 1.

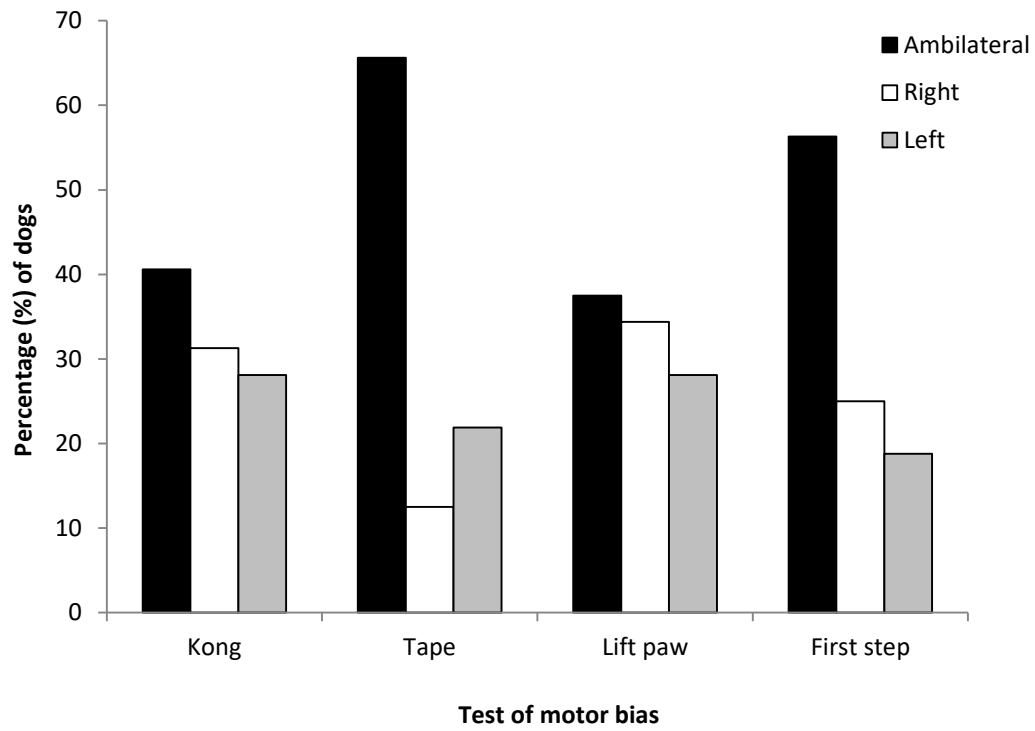


Figure 2.

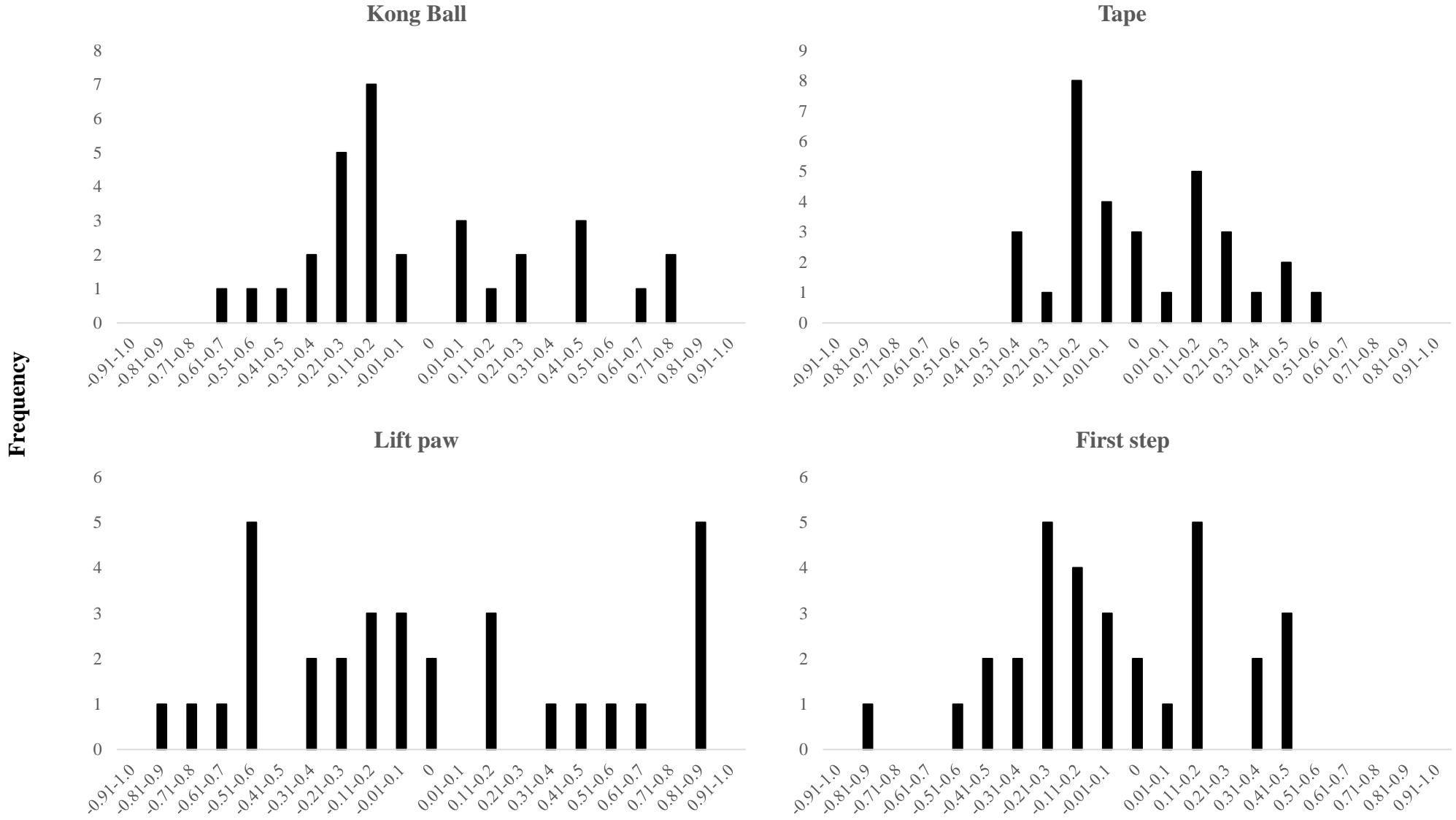


Figure 3.

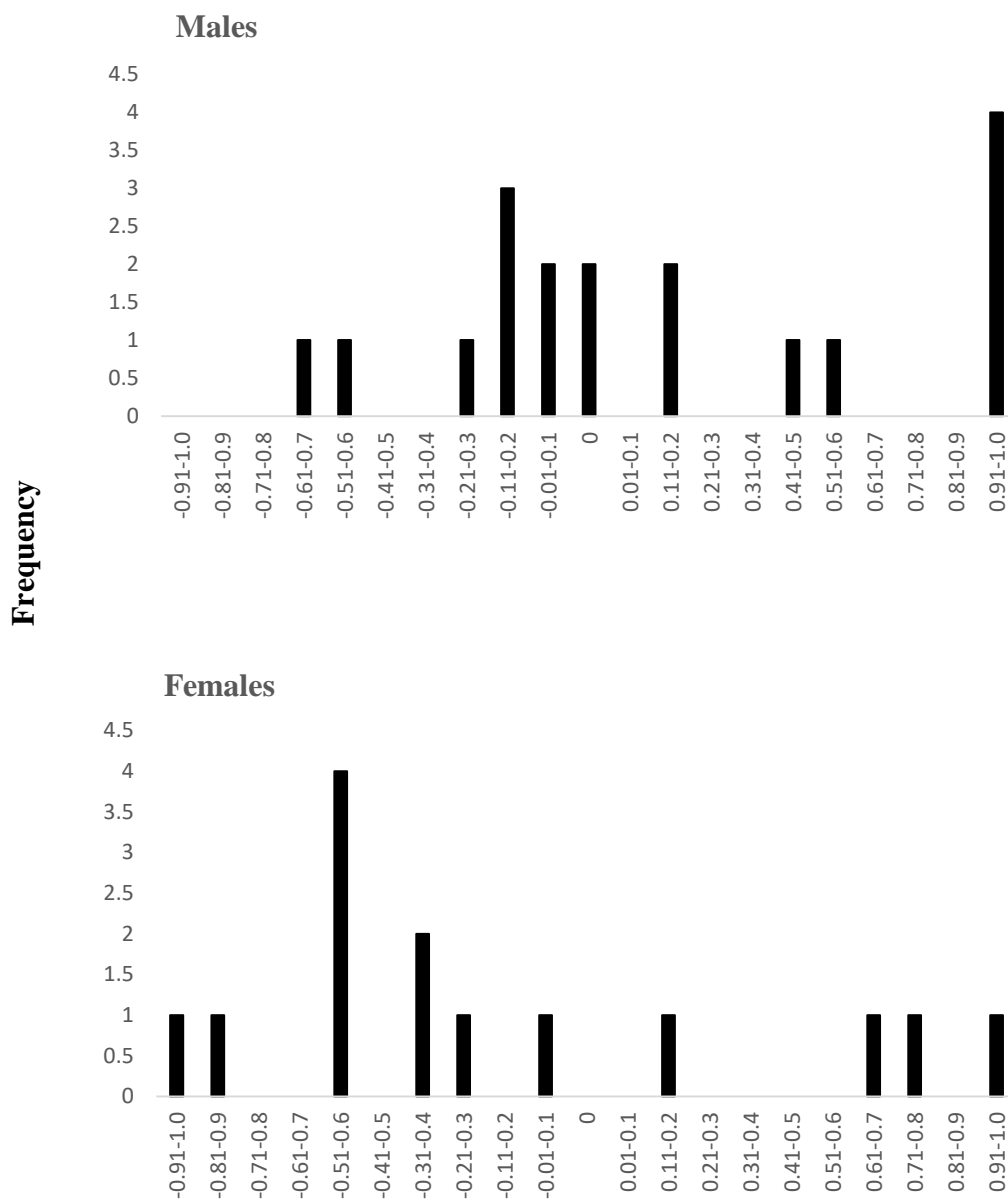


Figure 4.

