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Lateralisation of spontaneous behaviours in the domestic cat, *Felis silvestris*

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Running Headline: McDowell et al.: Lateralised behaviour in cats

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27 **ABSTRACT**

28 Recent years have drawn attention to the link between lateral bias and cerebral functional
29 asymmetry in animals. Most studies of animal laterality have focused on limb use arising
30 from forced experimental challenges as opposed to spontaneous behaviours. This study
31 explored, for the first time, the expression of lateralised spontaneous behaviour in the
32 domestic cat, a species that exhibits motor bias in the form of paw preferences. The side used
33 by 44 pet cats to perform three spontaneous behaviours (lying side, stepping down a flight of
34 stairs, stepping over a raised object) was recorded. Paw preferences were also assessed using
35 a more traditional forced food reaching challenge. Cats showed a significant lateral bias for
36 food reaching (73%), stepping down (70%) and stepping over (66%). Paw-preferent animals,
37 however, did not differ significantly in their tendency towards left- or right-sidedness. The
38 direction of the cats' side preferences was significantly correlated for most of the measures,
39 whether forced or spontaneous. The strength of the cats' motor bias was significantly related
40 to task; animals displayed a weaker lateral bias for lying side than any of the other measures.
41 The study revealed a sex split in the direction, although not the strength, of the cats' lateral
42 bias for food reaching, stepping down and stepping over. Male animals showed a significant
43 preference for using their left paw on these measures, while females were more inclined
44 towards right-sidedness. The study provides the first evidence that the domestic cat displays
45 motor laterality on specific spontaneous behaviours, and that the direction, although not the
46 strength, of these lateral biases is largely consistent with that of an experimental task. The
47 results suggest that the more forced food reaching test traditionally used to assess motor bias
48 in the cat offers a biologically valid measure of limb use in this species.

49 *Keywords:* behaviour; cats; handedness; laterality; paw preferences; sex differences

50

51 **INTRODUCTION**

52 One of the most prevalent features of human behaviour is motor laterality, defined as the
53 preferred use of one limb over another (e.g., Harris, 1983; Springer & Deutsch, 1989). The
54 most obvious display of motor bias in humans is handedness. An estimated 90% of people
55 prefer to use their right hand for most activities, including tool-use, teeth brushing and
56 writing (Annett, 1985; Porac & Coren, 1981).

57

58 It was previously believed that lateralised behaviour was a uniquely human trait. Research
59 now indicates, however, that many species of animal (e.g., amphibians, rodents, cats,
60 primates, marsupials, whales) display lateralised motor behaviours. This has led to
61 suggestions that lateral bias may be a universal phenomenon (for reviews see Frasnelli,
62 Vallortigara & Rogers, 2012; MacNeilage, Rogers & Vallortigara, 2009; Rogers, 2002;
63 Rogers, Vallortigara & Andrew, 2013; Vallortigara, Chiandetti & Sovrano, 2010;
64 Vallortigara & Rogers, 2005), although whether this exists at the level of group in animals, or
65 is related to other aspects of brain asymmetry, is still unclear (see reviews by Corballis, 2009;
66 Rogers, 2009; Vallortigara & Versace, 2017; Versace & Vallortigara, 2015).

67

68 Studies in the area of animal laterality have typically focused their attention on experiments
69 involving forced tasks, notably food reaching. However, a smaller number of investigations
70 have explored the directionality of more spontaneous expressions of animal behaviour.
71 Studies have focused on behaviours including the side used for foraging and feeding
72 (gorillas- Byrne & Byrne, 1991; Tabiowo & Forrester, 2013; humpback whales- Canning et
73 al., 2011; Clapham, Leimkuhler, Gray & Mattila, 1995; Woodward & Winn, 2006; walruses-
74 Levermann, Galatius, Ehlme, Rysgaard & Born, 2003), the limb employed to initiate
75 movement (horses- Lucidi et al., 2013; McGreevy & Rogers, 2005; giraffes- Svoke, 2017;

76 dogs- Hackert, Maes, Herbin, Libourel, & Abourachid, 2008; Tomkins, Thomson, &
77 McGreevy, 2010), grooming (chimpanzees- Marchant & McGrew, 1996), infant cradling
78 (chimpanzees- Manning & Chamberlain, 1994; Toback, 1999), clapping (chimpanzees-
79 Fletcher, 2006), suckling (horses- Komarkova & Bartosova, 2013; zebra- Pluhacek al. 2013),
80 hemifield use (birds- Ventolini, Ferrero, Sponza, Chiesa, Zucca & Vallortigara, 2005),
81 turning behaviour (sheep- Versace, Morgante, Pulina & Vallortigara, 2007), ground
82 scratching (chicks- Tommasi, 1999), and even urination (dogs- Gough & McGuire, 2015).
83 Many, although not all, of these studies suggest that lateral biases can be recorded
84 successfully from naturalistic observations of animal behaviour. What is less apparent is
85 whether these biases are consistent with those recorded experimentally using more forced
86 limb reaching tasks. Indeed, only a small number of studies, all involving primates
87 (Campbell's monkeys- Chapelain, Bec & Blois-Heulin, 2006, Chapelain et al., 2012; red-
88 capped mangabeys- Chapelain et al., 2012; red-fronted lemurs, Schnoell, Huebner, Kappeler
89 & Fichtel, 2014 common marmosets- Hook & Rogers, 2008;), have compared motor
90 preferences using these two methodological approaches. Two of the studies (Chapelain et al.,
91 2006; Schnoell et al., 2014) found that the expression of manual laterality was weaker in
92 naturally occurring behaviours (e.g., holding branches, self-grooming, feeding) compared to
93 forced limb use on an experimental task. Such findings are in line with the hypothesis
94 proposed by Warren (1980) which states that hand preferences should be stronger and more
95 rigid in experimental conditions on the basis that laterality is an artificial phenomenon
96 created by such situations. Moreover, Schnoell and others (2014) argue that a strong manual
97 bias for spontaneous actions may not be ecologically relevant for some species, particularly if
98 both hands are needed to ensure health and safety, e.g., swinging across trees. Nevertheless,
99 it seems that studying manual preferences on both experimental tasks and spontaneous
100 behaviours may provide more realistic and ecologically valid insights into the evolution and

101 significance of lateral biases in an animal's daily life than the use of only one methodological
102 approach.

103

104 The following study explored the expression of lateralised spontaneous behaviour in the
105 domestic cat, *Felis silvestris*, a species that has been shown to exhibit motor bias in the form
106 of paw preferences (e.g., McDowell, Wells & Hepper, 2016; Pike & Maitland, 1997; Wells &
107 Millsopp, 2009, 2012). We recorded the limb or side used by 44 pet cats to perform three
108 spontaneous (i.e., unforced) behaviours (lying side, stepping down a flight of stairs, stepping
109 over a raised object). Each animal's paw preferences were also assessed using a more
110 traditional forced food reaching challenge (McDowell et al., 2016). The study aimed to
111 identify whether asymmetries are consistent using two methodological approaches and
112 determine whether spontaneous expressions of natural behaviour can be used as a reliable
113 indicator of cerebral asymmetry in the cat.

114

115 **METHODS**

116

117 *Subjects*

118 Forty-four neutered pet cats (24 male, 20 female), of mixed breed, aged between 1-17 years
119 (mean age=3.98 +/- 0.56 years), participated in the study. For the purpose of analysis (see
120 later), the age of the cats was categorised as ‘young’ (defined as animals between 1-6 years of
121 age) and ‘old’ (defined as animals between 6-17 years of age). There was no significant
122 difference in the distribution of male and female animals in the two age groups ($\chi^2_1=3.26$,
123 $p=0.08$). All of the cats were family pets whose owners had consented to them participating
124 in the study. None of the cats had undergone any behavioural training, nor had any disability
125 or behavioural problem preventing them from completing the study.

126

127 *Laterality measures*

128 Cats’ lateral preferences were assessed using two approaches, namely, an experimental food
129 reaching test and observations of 3 spontaneous behaviours:

130

131 Food reaching test

132 Cats’ paw preferences for food reaching were assessed using the Catit Senses Food Maze
133 (Catit, UK). This maze is a 35.6cm tall spherical feeding ‘tower’, comprising 3 levels into
134 which food can be placed. The food is accessed via 3 holes on each level (see Figure 1 and
135 <https://www.catit.com/uk/shop/senses-2-food-tree>). For the purpose of this study, the top
136 level of the food maze was removed as it proved too high for the cats to put their paws into
137 without standing on their rear legs and compromising balance. The Catit has been used
138 successfully to record cats’ paw preferences (McDowell et al., 2016), and demonstrates good
139 test-retest reliability (McDowell, 2017).

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(Figure 1 about here)

Spontaneous behaviours

Three spontaneous behaviours were recorded:

i) *Lying side*

Lying side has been studied as a measure of lateral bias in quadrupedal species including dairy cattle (e.g., Tucker, Cox, Weary & Spinka, 2009) and sheep (Lane & Phillips, 2004). Cats typically lie on one side of their body while resting or sleeping. For this study, owners were required to record whether their cat lay down on their left or right side for each occurrence of this behaviour.

ii) *Step down*

The “First-stepping” task has been used to successfully measure paw preference in dogs (Tomkins et al., 2010). For this study, owners were required to record the paw (left or right) first used by their pet to descend their indoor set of stairs.

iii) *Step over*

Many cats use a litter tray for urination and/or defecation (Crowell-Davis, Curtis & Knowles, 2004). As this is often a tray with a slightly raised perimeter, the cat must lift one of its forelimbs to step into it. For the purpose of this study, owners were therefore required to record the paw first used by their cat to enter their litter tray.

To ensure familiarity with the three spontaneous behaviours and increase the objectivity of measures between subjects, the cats’ owners were provided with an information sheet

165 describing the actions they should expect to witness in their pet. Any spontaneous
166 occurrences of the behaviours made by the subject cats were also pointed out to the owners at
167 the time of the Experimenter's visit to their homes. In addition, pictures depicting cats
168 showing the three activities were presented to the owners. It was made clear that an animals'
169 use of both paws simultaneously should not be recorded. Owners were contacted once a
170 week to ensure compliance with the protocol and address any concerns.

171

172 *Procedure*

173 All of the subjects were tested individually in their own home environment. Each cat was
174 initially required to undertake the experimental *food reaching* test. Prior to the start of the
175 first trial, the cat was shown, and allowed to sniff, the food treat (Dreamies, Mars Petcare,
176 UK - small squares of cheese flavored cat treats). As the cat watched, 10 treats were placed
177 on the top (i.e., second) level of the food maze. Since the food could be accessed through 3
178 holes, it was ensured that the cat was placed directly in front of one hole for each trial. As
179 and when required (i.e., once all the food treats had been accessed by the cat), another 10
180 treats were placed in the food maze. A single trial comprised the cat placing its paw inside
181 the food maze and attempting to remove the treat. Only once the paw had been removed from
182 the maze did the next trial begin. The paw the cat used to attempt food retrieval, regardless of
183 whether or not a treat was retrieved, was recorded. Testing was carried out on a daily basis
184 until 50 responses were made. An average of 15 trials were carried out by each cat every day
185 to avoid the animals becoming bored, tired or stressed. No reward, be it tactile (comforting,
186 stroking) or social (verbal praise or smiling), was provided during the task.

187

188 Laterality data on the cats' spontaneous behaviours were collected by the subjects' owners
189 over a period of 3 months. Owners were given a score sheet and asked to record each

190 occurrence of the 3 spontaneous behaviours outlined above. The occurrence of 50 (left plus
191 right) expressions of each of the three spontaneous behaviours (*lying side, step down, step*
192 *over*) was recorded for each subject. Between 15-20 occurrences of each behaviour were
193 recorded per month by each cats' owner. Data were collected over a range of observation
194 sessions (e.g., in the morning, afternoon and evening) for each animal to reduce the
195 likelihood of interference from either one-off, or very habitual, events.

196

197 *Statistical Analysis*

198 Fifty data points per animal were recorded for each of the laterality measures (*food reaching,*
199 *lying side, step down, step over*). Binomial z -scores were calculated to determine whether the
200 frequency of right- or left-side use exceeded that expected by chance for each of the
201 measures. An alpha value of 0.05 was adopted for all analyses. A z -score greater than +1.96
202 (two-tailed) reflected a significant left paw preference, whilst a z -score less than -1.96
203 indicated a significant right paw preference. Cats with z -scores between +1.96 and -1.96
204 were classified as ambilateral.

205

206 A directional handedness index (HI) was calculated (see Wells, 2003) to quantify each cat's
207 lateral preference for each measure on a continuum from strongly left-side preferent (+1) to
208 strongly right side-preferent (-1). The HI was calculated by dividing the difference between
209 the total number of left and right side uses by their sum $(L-R)/(L+R)$. A mixed-design
210 ANOVA for the between-subjects factors of feline sex (*male, female*) and age (*young, old*)
211 and the within-subjects factor of task (*food reaching, lying side, step down, step over*) was
212 carried out to determine whether the direction of the cats' side preferences differed between
213 the tasks or was influenced by the animals' sex or age.

214

215 The strength of the cats' lateral preferences was calculated by taking the absolute value of
216 each HI score (ABS-HI) for each measure. A mixed-design ANOVA for the between-
217 subjects factors of feline sex (*male, female*) and age (*young, old*) and the within-subjects
218 factor of task (*food reaching, lying side, step down, step over*) was carried out to determine
219 whether the strength of the cats' side preferences differed between the tasks or was
220 influenced by the animals' sex or age.

221

222 Finally, Pearson product moment correlations were conducted to compare both the direction
223 (HI scores) and strength (ABS-HI scores) of lateral bias across the four tasks to explore for
224 any consistencies in strength and/or direction of motor asymmetry.

225

226 ***Ethical Note***

227 All methods adhered to the Association for the Study of Animal Behaviour/ Animal Behavior
228 Society Guidelines for the Use of Animals in Research (Association for the Study of Animal
229 Behaviour, 2006). Ethical approval for the study was granted by the Research Ethics
230 Committee, School of Psychology, QUB. All of the cats' owners were required to complete a
231 written consent form at the time of subject recruitment. Owners were fully informed in
232 writing of the study's purpose and advised that they were free to leave the project and have
233 their pets' data withdrawn at any time. To minimise stress to the cats, data were collected in
234 the subjects' own homes. Animals' paw preferences on the food reaching test were collected
235 over an average of 3 days to minimise the risk of inducing tiredness or stress.

236

237 **RESULTS**

238

239 *Distribution of lateral bias*

240

241 Food reaching

242 The distribution of the cats' paw preferences on the food reaching test was not significantly
243 different to that expected by chance alone ($\chi^2_2=1.27$, $P=0.53$). Significantly ($P=0.003$,
244 binomial test) more cats had a paw preference ($N=32$, 72.7%) than were ambilateral ($N=12$,
245 27.3%), however the paw-preferent cats were no more likely to be left- ($N=18$, 56.2%) than
246 right- ($N=14$, 43.8%) pawed ($P>0.05$, binomial test) [Figure 2].

247

248 Lying side

249 Analysis revealed that 4 (9.1%) cats preferred to consistently lie on their left side, 7 (15.9%)
250 preferred to lie on their right side, while 33 (75.0%) were ambilateral for this behaviour
251 (Figure 2). This distribution of lateral bias was significantly different to that expected by
252 chance alone ($\chi^2_2=34.68$, $P<0.001$). Significantly ($P=0.001$, binomial test) more cats were
253 ambilateral than side-preferent, but side-preferent cats were no more likely to exhibit a left
254 than right side preference for this behaviour ($P>0.05$, binomial test).

255

256 Step down

257 Fifteen (34.1%) cats were reported to consistently use their left paw to step down a flight of
258 stairs, 16 (36.4%) to use their right paw, while 13 (29.5%) animals were ambilateral (Figure
259 2). This distribution of paw use did not differ significantly ($\chi^2_2=0.32$, $p=0.85$). Significantly
260 ($P=0.010$, binomial test) more cats were paw-preferent than ambilateral for this behaviour,

261 however paw-preferent cats were no more likely to be left- than right-pawed ($P>0.05$,
262 binomial test).

263

264 Step over

265 Sixteen (36.4%) of the subjects were reported to consistently use their left paw to step over,
266 13 (29.5%) to use their right paw and 15 (34.1%) showed no paw preference (Figure 2). This
267 distribution of paw preference was not significantly different to that expected by chance
268 alone ($\chi^2_2=0.32$, $p=0.85$). Significantly ($P=0.04$, binomial test) more cats were paw-preferent
269 for this behaviour than ambilateral, however paw-preferent cats were no more likely to be
270 left- than right-pawed ($P>0.05$, binomial test).

271

272 (Figure 2 about here)

273

274 *Direction of lateral bias*

275 A mixed-design ANOVA revealed no significant effect of task ($F_{3,120}=1.03$, $P=0.38$) on the
276 direction of the cats' motor bias. This measure was significantly related to feline sex
277 ($F_{1,40}=5.15$, $P=0.02$), with males favouring their left side (mean HI= 0.15 +/- 0.07) and
278 females preferring their right side (mean HI= -0.12 +/- 0.07). The age of the cats was
279 unrelated to the direction of the animals' motor bias ($F_{1,40}=0.11$, $P=0.74$).

280

281 There was a significant positive correlation in the direction of the cats' lateral bias between
282 the *food reaching* test and all of the three spontaneous behaviours [P values corrected for
283 multiple comparisons] (*lying side*, $R_{44}=0.38$, C.I.=0.09-0.67, $P<0.05$, *step down*, $R_{44}=0.61$,
284 C.I.=0.37-0.86, $P<0.001$, *step over*, $R_{44}=0.54$, C.I.=0.28-0.80, $P<0.001$). HI scores for the
285 *step down* and *step over* tests were also significantly correlated ($R_{44}=0.58$, C.I.=0.33-0.84,

286 $P<0.001$). There was no significant correlation in the direction of the cats' motor preferences
287 for behaviours of *lying side* and *step down* ($R_{44}=0.28$, C.I.=-0.02-0.58, $P=0.06$) or *step over*
288 ($R_{44}=0.25$, C.I.=-0.48-0.13, $P=0.10$).

289

290 *Strength of lateral bias*

291 The strength of the cats' lateral bias differed significantly between the tasks ($F_{3,120}=4.49$,
292 $P=0.005$). Post-hoc paired t -tests (with P values corrected for multiple comparisons) showed
293 that cats displayed a significantly weaker lateral bias for *lying side* (mean ABS-HI= 0.20 +/-
294 0.02) than for *food reaching* ($t_{43}=7.09$, $P<0.001$; mean ABS-HI= 0.50 +/- 0.04), *step down*
295 ($t_{43}=7.09$, $P<0.001$; mean ABS-HI= 0.44 +/- 0.03) and *step over* ($t_{43}=-4.5$, $P<0.001$; mean
296 ABS-HI= 0.40 +/- 0.04).

297

298 Analysis revealed no significant effect of feline sex ($F_{1,40}=0.31$, $P=0.58$) or age ($F_{1,40}=0.31$,
299 $P=0.85$) on the strength of the animals' lateral bias

300

301 There was a significant positive correlation in the strength of the cats' paw use for the
302 behaviours of *step down* and *step over* ($R_{44}=0.50$, C.I.=0.22-0.76, $P<0.001$). None of the
303 other behaviours were significantly correlated for strength of motor bias ($P>0.05$).

304

305 **DISCUSSION**

306 The results from this study provide the first evidence that certain spontaneous behaviours,
307 notably those involving limb use, are lateralised in the domestic cat. The study also suggests
308 that food reaching tests, commonly used to assess paw preference in the cat, offer an
309 ecologically valid measure of laterality for this species.

310

311 The majority of cats in the present study showed a lateral bias on the measures involving paw
312 use, i.e., *food reaching* (73%), *step down* (70%) and *step over* (66%). Paw-preferent animals,
313 however, did not differ significantly in their tendency towards left- or right-sidedness.
314 Previous studies have reported a roughly similar distribution of lateralisation in cats tested on
315 a range of challenges designed to assess paw preference (Pike & Maitland, 1997; Tan &
316 Kutlu, 1991; Tan, Yaprak & Kutlu, 1990; Wells & Millsopp, 2009, 2012), and, together,
317 point strongly to paw use at the level of the individual for this species. The spontaneous
318 behaviour of *lying side*, the only measure that did not concentrate on paw use, was not found
319 to be lateralised, with only 25% of the subjects exhibiting a significant side preference for
320 this activity. With this in mind, future studies on feline laterality may be wiser to focus their
321 attention on behaviours involving limb use, which appear to be more reflective of
322 hemispheric specialisation in the cat.

323

324 The cats' HI scores were found to be significantly correlated for most of the measures in this
325 study, whether forced or spontaneous. Previous experiments have yielded mixed results
326 regarding the consistency of motor bias on experimental tasks *vs.* expressions of spontaneous
327 behaviours, with some authors pointing to a significant relationship between such measures
328 (Chapelain et al., 2012), and yet others unearthing no evidence of an association (Chapelain
329 et al., 2006; Schnoell et al., 2014). Much appears to depend on the nature of the measures

330 under scrutiny. Studies which have isolated a specific spontaneous action have reported more
331 consistent patterns of motor bias between experimental tasks and natural behaviours than
332 those that have combined very different actions. For instance, Chapelain and associates
333 (2012) found consistency in reaching for an object (food) both spontaneously and in a more
334 forced experimental set-up in both red-capped mangabeys and Campbell's monkeys. By
335 contrast, Schnoell and colleagues (2014) reported no consistency in the hand use of red-
336 fronted lemurs on a forced food reaching task compared to the expression of 5 spontaneous
337 actions, e.g., allogrooming, autogrooming, warding off conspecifics. It may be more
338 beneficial and methodologically valid to focus on one specific spontaneous behaviour to get a
339 clearer representation of natural laterality, although deciding on an adequate measure has
340 proven difficult (e.g., Marchant & McGrew, 1996). Studies on primates have shown that
341 animals often only show lateralised hand use for specific spontaneous actions, e.g., feeding
342 (Meguerditchian et al., 2010; Tabiowo & Forrester, 2013), whilst others, often those for
343 which there is no biological value to be gained from lateralisation (e.g., lying side, as
344 reflected in the present study), are more likely to be ambilateral in nature.

345

346 The strength of the cats' motor bias was found to be related to task, with animals displaying a
347 significantly weaker lateral bias for *lying side* than any of the other measures. However,
348 strength of paw preference did not differ significantly between the *food reaching*, *step down*
349 or *step over* tests, as might have been expected. It has been argued that the synthetic nature
350 of an experimental task can create artificially stronger motor asymmetries (Warren, 1980);
351 limb preferences tend to be less flexible on forced tasks, and are perhaps more readily
352 reinforced, e.g., by food treats. In a similar vein, the 'task complexity' hypothesis argues that
353 more complex actions, which tend to demand the use of one hemisphere over the other,
354 typically result in a stronger motor bias (Fagot & Vauclair, 1991). These theories may

355 explain why the cats in the present study were more weakly lateralised for the spontaneous
356 behaviour of *lying side*, the least demanding motor challenge. However, they do not
357 necessarily explain why the cats showed no stronger a paw preference on the food reaching
358 task. The findings suggest that limb use on a forced experimental challenge may not be an
359 artificial phenomenon, but may, rather, be an ecologically reliable indicator of motor bias for
360 the domestic cat. The findings also lend support for the suggestion that task specific cues
361 (e.g., postural support, task complexity) may not influence manual laterality in non-primate
362 mammals (Konerding, Hedrich, Bleich, & Zimmerman, 2012).

363

364 The study revealed a sex split in the direction, although not the strength, of the cats' lateral
365 bias on the *food reaching* task and two of the three spontaneous behaviours (*step down* and
366 *step over*). In all cases, male animals showed a significant preference for using their left paw,
367 while females were more inclined to exhibit a right-sided bias. This sex split has been found
368 previously in cats (Wells & Millsopp, 2009, 2012) and other species, e.g., dogs (Quaranta,
369 Siniscalchi, Frate & Vallortigara, 2004; Wells, 2003), horses (Murphy, Sutherland, & Arkins,
370 2005). It is the first time, however, that spontaneous actions have been shown to be related to
371 feline sex. Interestingly, the few studies that have reported differences between male and
372 female animals for naturalistic behaviours have demonstrated a directional effect similar to
373 that observed in this experiment for some tasks (black and white snub-nosed monkeys, *Pan*,
374 Xiao & Zhao, 2011; lemurs, Ward, Milliken, Dodson, Stafford & Wallace, 1990). It has been
375 argued that naturalistic behaviours encouraged the evolution of cerebral specialisation for
376 motor dominance (Forrester et al., 2013). Assuming this is the case, a sex split would not
377 necessarily be expected for spontaneous actions. Indeed, it would be more efficient and
378 generally advantageous for a species to demonstrate population-level laterality for

379 spontaneous expressions of behaviour (e.g., Ghirlanda, Frasnelli & Vallortigara, 2009;
380 Ghirlanda & Vallortigara, 2004).

381

382 In some respects, it is surprising that a sex effect was discovered in this study, since the
383 sample was comprised entirely of castrated animals. Studies on dogs have failed to report an
384 effect of canine sex on paw preferences in samples of neutered, or a mixture of de-sexed and
385 entire, animals (Batt, Batt, Baguley & McGreevy, 2008; Branson & Rogers, 2006; Schneider,
386 Delfabbro & Burns, 2013; Wells, Hepper, Milligan & Barnard, 2017); this has led the authors
387 to argue that a hormonal factor may be at play in shaping motor bias. Further work is needed
388 to investigate this, but the strong sex effects reported here, and elsewhere, both on
389 experimental challenges and expressions of spontaneous behaviour, and using both castrated
390 and de-sexed populations, point more and more strongly to underlying differences in the
391 neural architecture of male and female cats. This is perhaps not surprising, given the sex
392 differences in brain asymmetries reported across species (see Bianki & Filippova, 2001).

393

394 Some authors have reported relative stability in preferred limb use across the lifespan in
395 nonhuman species, notably primates (e.g., Hook & Rogers, 2000; Stafford, Milliken & Ward,
396 1990). There was no evidence from the present investigation that paw use differed between
397 the younger and older cohorts of cat. In their earlier studies, Wells and Millsopp (2012)
398 found that cats' paw preferences differ significantly over the course of their first year of life,
399 stabilising thereafter. The youngest cats in the present study were 1 year of age, no doubt
400 explaining the lack of any significant age effects. The findings from this study lend further
401 support for the idea that cats, like others species, show stability in paw preferences across
402 adulthood, even in the display of naturalistic behaviours.

403

404 *Conclusions*

405 The findings from this study provide the first evidence that the domestic cat displays motor
406 laterality on specific spontaneous behaviours, notably those involving limb use, and that the
407 direction of these lateral biases is largely consistent with that of an experimental task. The
408 results suggest that the more forced food reaching tests traditionally used to assess motor bias
409 in the cat offer a biologically valid measure of limb use in this species. It is clear that both
410 context and relevance of lateralisation of particular behaviours are important factors which
411 need to be considered when interpreting the results from investigations of this nature.
412 However, it could be argued that exploring lateral bias on an experimental task, as well as
413 spontaneous expressions of behaviour, may provide more realistic insights into the evolution
414 and importance of lateral bias in an animal's daily life than the use of just one methodological
415 approach. Future studies may also consider exploring other forms of lateral bias in addition
416 to limb preferences as an indicator of cerebral asymmetry. Feral horses, for example, have
417 been found to display significant eye preferences in the absence of a limb bias (Austin &
418 Rogers, 2012), while common marmosets show a strong bias at the level of the group for eye
419 use, but not hand preference (Hook & Rogers, 1998). Exploring lateral biases beyond limb
420 preference may further our understanding of cerebral functioning in nonhuman species.

421

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591

592 **Figure Legends**

593

594 Figure 1. The Catit Food Maze used for the food-reaching test (see also
595 <https://www.catit.com/uk/shop/senses-2-food-tree>)

596

597 Figure 2. Distribution of lateral bias across the four measures

Figure 1



Figure 2

