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49 LIMB PREFERENCE IN THE GALLOP OF DOGS AND
50 THE HALF-BOUND OF PIKAS ON FLAT GROUND

51
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56
57 **Abstract** - During fast locomotion — gallop, half bound — of quadruped mammals, the ground contact of
58 the limbs in each pair do not alternate symmetrically. Animals using such asymmetrical gait thus choose
59 whether the left or the right limb will contact the ground first, and this gives rise to limb preference. Here,
60 we report that dogs (Mammalia, Carnivora) and pikas (Mammalia, Lagomorpha) prefer one forelimb as
61 trailing limb and use it as such almost twice as often as the other. We also show that this choice depends on
62 the individual and is not a characteristic of the species, and that the strength of the preference was not
63 dependent on the animal's running speed.
64

65 **Keyword:** handedness, quadruped, locomotion, laterality, asymmetrical gaits, Carnivora, Lagomorpha,
66 stability.
67

68 INTRODUCTION

69 The expression of brain lateralization has been observed in behaviours as different as feeding, manipulation,
70 and communication in several families of vertebrates. Limb preference is a subset of this expression and has
71 been documented in birds and in most families of tetrapods including toads, anurans and mammals (for review
72 in Vallortigara et al., 1999). In some species, sex was identified as a determinant of the direction of the
73 preference at population level (in dogs: Wells, 2003; Quaranta et al., 2004; Poyser et al., 2006; in cats: Tan et
74 al., 1990) but not of the strength of preference. The strength of preference is thought to be task dependent and
75 increases as tasks require more cognitive function (Fagot and Vauclair, 1991) and coordination (Hopkins,
76 1995).

77 Curiously, limb preference during locomotion has not been extensively explored, although locomotion is the
78 primary function of limbs. Malashichev (2006) observed five species of anuran and found a limb preference in
79 those that exhibit an “alternated limb locomotion or other unilateral limb activity”. He suggested that the
80 degree of lateralization in the motor response depends on the mode of locomotion used by a species. In the
81 asymmetrical gaits of mammals— i.e. gallop, bound, and half-bound — the fore and hind pairs of legs make
82 contact with the ground alternately. During gallops or half-bounds, the motions of the two limbs of a pair are
83 not symmetrically alternated, such that one limb of each pair touches the ground first and is called the *trailing*
84 limb, the other one is called *leading* limb. The trailing and leading limb of each pair cannot be systematically
85 assigned to the left or right limb because during locomotion animals switch trailing and leading limbs from
86 time to time. In their study of the gallop of four race horses, Deuel and Lawrence (1987) compared the
87 kinematics of trailing and leading limbs. All the horses preferred the right limb as trailing limb. Moreover, the
88 duration of the stance phase of the trailing forelimb differed significantly according to whether it was the right

89 or the left limb. Walter and Carrier (2007) observed that four of the six dogs in their study preferred one limb
90 as the trailing limb during gallop. Finally, Hook and Rogers (2002) found that marmosets land preferentially
91 with the right limb and that the choice of this limb is correlated with the leading limb used during leaping and
92 walking.

93 There have been few quantitative studies of the direction or the strength of limb preference during animal
94 locomotion. We therefore investigated this issue and changes in laterality with speed in dogs and pikas, two
95 mammals with different morphologies, behaviours and gaits. Dogs are medium-sized digitigrades that trot over
96 a large range of speeds before switching to galloping at high speeds. In contrast, pikas are small plantigrades
97 that switch to half-bound locomotion for all speeds faster than walking (Gambaryan, 1974; Fischer and
98 Lehmann, 1998).

99 ANIMALS AND METHODS

100 We studied five dogs (*Canis familiaris*, Mammalia: Carnivora) and four pikas (*Ochotona rufescens*,
101 Mammalia: Lagomorpha). The dogs were male Belgian shepherd malinois of similar size (withers
102 height= 0.61 ± 0.05 m, BW= 28.3 ± 2.0 kg); they belonged to the French army and were thus healthy, obedient,
103 and used to energetic exercise. Pikas (withers height= 0.05 m, body length= 0.16 m, BW=150-200 g) were
104 reared at the IPBS (CNRS, Toulouse) by A. Puget and were kept at the Motion Lab, University of Iena,
105 Germany; they were reared and used in conformity with German animal welfare regulations.

106 *Methods*

107 Dogs were studied while running outdoors along a 1 m x 12 m long carpet graduated each 10 cm for stride
108 length calculations. They were filmed with a high speed camera (Basler A504K, highland Illinois, USA)
109 positioned 8 m from the left-hand side of the carpet and driven at 200 Hz. The camera was also driven to
110 maintain the dog in the field of view (about 3 m). Under outdoor conditions – in contrast to treadmill —the
111 animal's speed is not controlled and the collected locomotor cycles depend largely on the performance and
112 motivation of the dog. The dog handler ran the distance at five different speeds to allow the dogs to gallop at
113 different speeds. Dogs were all lead on a leash by the handler on the right-hand side. The two meters long
114 leash was light and long enough to avoid interfering with the dog's locomotion. To study speeds faster than
115 human running speed in a second series of records, dogs were also encouraged to run freely towards a ball at
116 the opposite end of the same carpet. We used this second series of records to test whether the handler had an
117 influence on the direction of the preference. The direction of preference for each dog was the same in trials
118 with and without the leash. Trials where the leash was bent or where the animal looked at the handler (very
119 rare because galloping quadruped mammals lock the degree of freedom of the neck) were excluded from our
120 data set. Animal speed was calculated from stride length and stride duration. Speeds were between 2.2 m/s and
121 10.3 m/s and each sequence contained 4-8 locomotor cycles according to speed. However, each dog did not
122 cover exactly the same range of speeds.

123

124 Pikas ran on a treadmill and running speed was imposed on the animals. They were habituated to the
125 manipulation and to the running environment for 15 minutes per day for two weeks. High speed video films
126 were recorded with a CAMSYS® camera driven at 400 Hz and equipped with a Fujinon zoom-lens (1.2/75)
127 adjusted to cover one body length. Sequences of 4s were recorded at speeds between 1.2 m/s and 2.2 m/s, a
128 range of speeds comfortably achieved by the four animals. The speed was increased by 0.05 m/s between
129 consecutive sequences. Each sequence included between 15 and 30 locomotor cycles. Animal were allowed
130 rest for 3 minutes between the running sequences.

131
132 *Processing films and statistics*

133 We noted the limb used as the trailing limb in each locomotor cycle recorded on each film sequence; films
134 were each scored twice independently and readings compared. There was no disagreement associated with the
135 determination of the trailing limb.

136 However, assuming that the left/right distribution converges on a particular value as the number of cycles
137 analysed increased, the truncation of data acquisition after any given number of cycles would limit accuracy.
138 The power analysis module of statistical software (STATISTICA v.6, *Statsoft*) was used to determine the
139 accuracy according to the sample size.

140 We grouped our data into three classes of speed: slow (S), medium (M) and fast (F) gallop (or half-bound). As
141 the range of speed covered depended on the motivation of the dogs to perform the exercise, speed classes were
142 adapted to the performance of each dog by dividing the range of speed into three equal intervals for each
143 animal; thus, the classes differed between individuals. The limits of the classes are given in Fig.1. For pikas,
144 the three classes each had the same width [1.2-1.5] m/s, [1.5-1.8] m/s and [1.8-2.2] m/s; these classes have
145 biological relevance as pikas introduce a first aerial phase at about 1.5-1.6 m/s and then a second at around
146 1.8-1.9 m/s (Fischer and Lehmann, 1998; Hackert, 2003).

147 The significance of our binary (right/left) data was tested for each speed class using a χ^2 test (1 degree of
148 freedom) to detect a significant difference ($p < 0.05$) from a 50:50 distribution. Classes were then compared two
149 by two using a χ^2 test ($p < 0.05$, $H_0 =$ “distributions are different”).

150 A handedness index (HI) was calculated by subtracting the total number of left-trailing touch-downs (L) from
151 the total number of the right-trailing touch-downs (R) divided by the total number of trailing touch-downs: $(R$
152 $- L)/(R + L)$. The resulting values, ranging from -1.0 to 1.0, provide a score for each animal's hand preference
153 on a continuum from strongly left-handed to strongly right-handed. The absolute value of the HI (ABS-HI)
154 indicates the strength of hand preference, irrespective of its direction (see Hopkins, 1995).

155 RESULTS

156 Left- and right-handed individuals were found among dogs and pikas. In each speed class the 10 animals
157 significantly preferred ($p < 0.05$) one limb, except pika 4 and the slow classes of pika 1 and of dog 3 (fig. 1).
158 The direction of preference remained the same in the three speed classes for each animal. Comparing the

159 strength of limb preference of speed classes two by two, significant ($p < 0.05$) differences were observed only
160 between the slow class of pika 1 and the medium and fast classes, and between the fast class of pika 2 and the
161 slow and medium classes. Thus, we observed a constant strength of limb preference in 8 of 10 animals,
162 including both dogs and pikas. The strength of preference varied between individuals and was generally
163 stronger in dogs (ABS-HI from 0.31 to 1, mean ABS-HI= 0.65) than in pikas (ABS-HI from 0 to 0.46, mean
164 ABS-HI= 0.3).

165 DISCUSSION

166 Lateralized behaviour in dogs has been described (Tan, 1987; Wells, 2003; Quaranta et al. 2004; Van Alphen
167 et al., 2005; Poyser et al. 2006; Branson and Rogers, 2006) but not as concerns locomotion. Our study shows
168 that paw preference is present during asymmetrical locomotion in two quadrupeds: dogs and, for the first time,
169 a lagomorphian.

170 Previous studies report an influence of sex on the direction of the lateralization at the population level in dogs
171 (Quaranta et al., 2004) but not on the strength of the lateralization (Wells, 2003). Our group only included
172 adult males and was equally divided into right- and left-pawed dogs, but the small number of subjects studied
173 prevents conclusions at the population level.

174 The source of asymmetry in gallop and half-bound locomotion corresponds to a functional differentiation
175 between the trailing and leading limbs of a pair. Indeed, Walter and Carrier (2007) found significant
176 differences in the peak vertical forces of galloping dogs in the hind but not in the fore pair, a larger
177 decelerating impulse in the leading than trailing forelimb and a more accelerating impulse in the leading than
178 trailing hind limb. Hence, the specific exercises of each limb may lead to a specific muscular fatigue. To
179 minimize this muscular fatigue, animals often switch between trailing and leading limbs when galloping and
180 half-bounding. The strength of preference observed thus depends on the number of switches and the number of
181 consecutive cycles recorded in a locomotor sequence. In our study of dogs, sequences included 4-8
182 consecutive locomotor cycles; for pikas locomotor sequences involved 15-30 consecutive cycles, potentially
183 giving rise to more fatigue and consequently more switches. This methodological difference may have
184 contributed to the lower strength of preference observed in pikas.

185 Ecological factors certainly influence the strength of preference during gallop in a species. Using the data
186 published by Deuel and Lawrence (1987) concerning a group of four ridden race horses, all left footed (15
187 cycles recorded per horses), we calculated a mean HI of 0.32 (HI from 0.12 to 0.50). This is slightly higher
188 than the value we obtained for pikas but lower than that for dogs. This indicates that the strength of preference
189 does not correlate strongly with animal size. Possibly, the type of locomotion influences the strength of
190 lateralization: pikas, a model for many small mammals, do not plan their trajectory and therefore discover the
191 relief at the last moment. Manoeuvrability, i.e. the ability to suddenly turn left and right, and reactivity are
192 most important for prey species like pikas. In contrast, the locomotion of dogs and other carnivores is goal
193 directed because they gallop when pursuing prey; their locomotion is more cognitive. These two types of

194 locomotion correspond to two different tasks —escaping or hunting — and define a gradient of cognitive
195 involvement (Fagot and Vauclair, 1991). On this gradient, horses like pikas are prey, but with a much larger
196 field of view and so there is a larger cognitive input. Indeed, comparing species involves defining more
197 precisely the types of locomotion they use, and thus the types of task they perform.

198 In their study of manual laterality in non human primates, Fagot and Vauclair (1991) developed a
199 framework to classify tasks. They defined a gradient for the strength of lateralization according to the
200 complexity of the task. Complexity is here defined in terms of spatiotemporal precision of the movement and
201 novelty of the situation (inducing cognitive functions). They thus opposed complex *high level* tasks to *low*
202 *level* tasks including familiar practised activities that should require less cognitive involvement.

203 Different tasks have been given to dogs to explore the strength of their paw preference: for example
204 retrieving a chocolate from a can (mean ABS-HI=0.39; Wells, 2003), and holding a hollow cylinder filled with
205 food (Kong test; Branson and Rogers, 2006). In the latter experiment the ABS-HI values were between 0 and
206 0.8, with most falling between 0.1 and 0.5; we estimate that the mean ABS-HI value was around 0.35-0.40, a
207 value in accordance with the 0.39 found by Wells for the other task. The slightly lower value found for
208 removing an adhesive tape from the nose (mean ABS-HI about 0.30; Quaranta et al., 2004) appears natural
209 since the movement is directed towards a body part – the nose - and is thus more stereotyped i.e. familiar
210 comparable in some extent to cleaning movement. In contrast, removing a blanket from head required hand-
211 head coordination, and is thus a more complex task and this HI was found higher (mean ABS-HI=0.5; Wells,
212 2003). The mean ABS-HI values for all these idiomatic tasks falls between 0.3 and 0.5 despite large
213 variations at the individual level and notable differences in the composition of the groups of animals. For paw
214 lifting on command, Wells found, by contrast, a very high degree of lateralization (mean ABS-HI=0.8) but this
215 may have been due to learning reinforcement effects affecting performance. Thus, asymmetrical locomotion in
216 dogs (mean ABS-HI=0.65) seems to be subject to a strong preference, although there are methodological
217 issues to be considered when interpreting this finding.

218 Where does asymmetrical locomotion fall on the gradient defined by Fagot and Vauclair? Cyclic locomotion
219 on flat terrain is by nature the most stereotyped and practised movement and consequently belongs, *a priori*, to
220 the class of low level tasks. However, galloping *stably* sets constraints on the animal's motion: touching down
221 at the appropriate instant with the trailing limb improves the dynamic stability of running (Seyfarth et al.,
222 2003; Hackert, 2003; Fischer and Blickhan, 2006). The instant of touch-down of the limbs is tuned precisely
223 by the so-called pre-stance retraction of the trailing limb, i.e. the movement of rotation of the trailing limb
224 toward the ground before contact with it. This movement of rotation is a general characteristic of the
225 kinematics of bouncing and running: during the last instants of the swing phase, the shoulder blade initiates a
226 back rotation of the forelimb in many quadruped mammals (Fischer et al., 2002). Because of the requirement
227 for precision in the motion of the single limb, asymmetrical locomotion could be considered to be a high level
228 task.

229 Moreover, spatiotemporal coordination between the limbs of the pair (and between the pairs) makes
230 asymmetrical locomotion closer to bimanual manipulative tasks than unimanual task. The mean values of

231 ABS-HI in non human primates during bimanual manipulation are higher (ABS-HI=0.80 in a male group of
232 capuchin monkeys, *Cebus apella*, and 0.76 in a mixed group of white-faced capuchin monkeys, *Cebus*
233 *capucinus*) than during unimanual task, for example a reaching movement [mean ABS-HI=0.4 in Spinozzi et
234 al (1998) and 0.31 in Meunier and Vauclair (2007); note that the value for reaching movements in primates
235 and dogs are comparable]. Involving the familiar and repetitive aspects of galloping but also a requirement for
236 spatiotemporal precision and limb coordination, asymmetrical locomotion comes between low and high level
237 tasks as defined by Fagot and Vauclair (1991). Moreover, although a dynamic stable gallop requires a
238 threshold speed, an increase of speed only weakly enhances dynamic stability (Seyfarth et al, 2002). In
239 Bernstein's view, a fast gallop is as complex as a slow gallop, at least in the context of advancing in a straight
240 line on even terrain, because the number of degrees of freedom of the musculo-skeletal system to be controlled
241 is the same (Bernstein, 1984). Consistent with this view, we found that the strengths of preference were
242 independent of speed during galloping.

243 Asymmetrical gaits are a quasi exclusivity of mammals. The comparison of the morphology of the oldest
244 mammalian fossils with the morphology of extant small mammals indicates that the potential for such
245 asymmetrical locomotion was already present in early mammals (Ji et al., 2002). The introduction of
246 asymmetrical locomotion with a shift between forelimbs (gallop, half-bound) minimized the vertical
247 displacement of the centre of mass and thus led to more economic locomotion (Hackert, 2003). Moreover, the
248 functional differentiation between trailing and leading limb during asymmetrical locomotion gives rises to a
249 limb preference that may also reduce energetic cost. Indeed, torques that act in the preferred arm during
250 manipulative movements in humans are less than those in the other arm, as both arms performed the same task
251 by using the same trajectory (Bagesteiro and Sainburg, 2002). These observations lead us to suggest that limb
252 preference was present in the locomotion of early mammalian species. The ability to perform precise and/or
253 powerful manipulations may have sustained the lateralization of brain organization through evolution
254 (Vallortigara et al., 1999; Rogers and Andrew, 2002; Vallortigara and Bisazza, 2002; Bradshaw and Rogers,
255 1993), so it is plausible that the benefits of an asymmetrical gait for efficient locomotion may also have
256 sustained lateralization.

257

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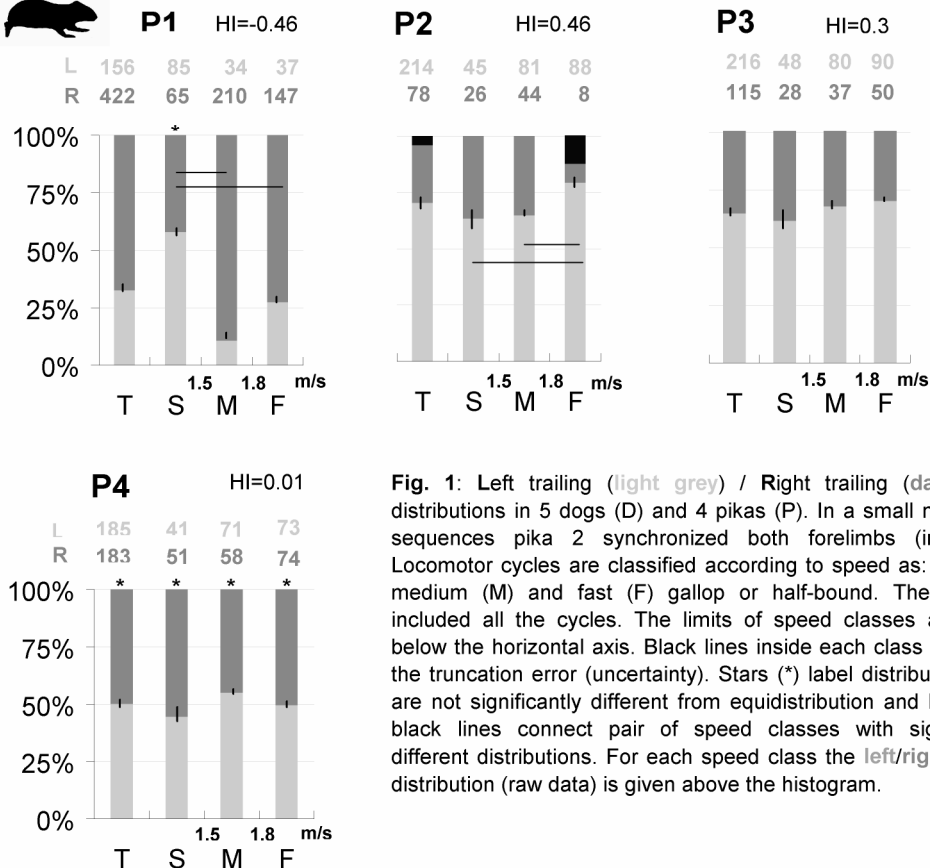
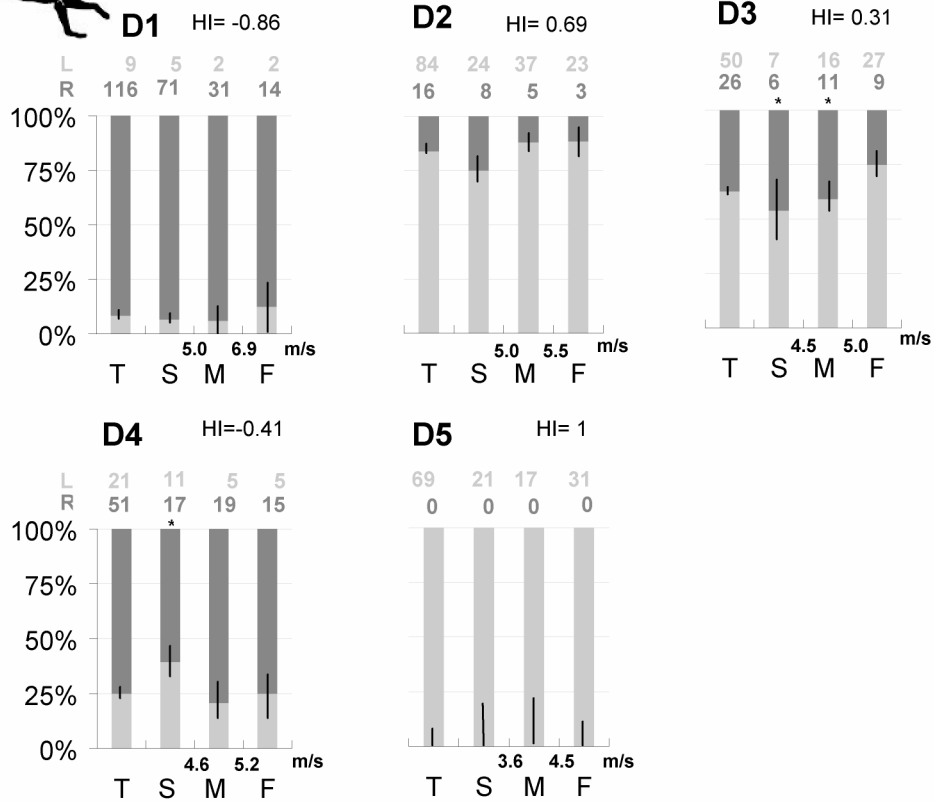


Fig. 1: Left trailing (light grey) / Right trailing (dark grey) distributions in 5 dogs (D) and 4 pikas (P). In a small number of sequences pika 2 synchronized both forelimbs (in black). Locomotor cycles are classified according to speed as: slow (S), medium (M) and fast (F) gallop or half-bound. The T class included all the cycles. The limits of speed classes are given below the horizontal axis. Black lines inside each class represent the truncation error (uncertainty). Stars (*) label distributions that are not significantly different from equidistribution and horizontal black lines connect pair of speed classes with significantly different distributions. For each speed class the left/right trailing distribution (raw data) is given above the histogram.