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Motor asymmetry in goats during a stepping task

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ABSTRACT

Behavioural laterization consists of perceptual and motor lateralization and provides adaptive advantages such as a general increase in brain efficiency. Motor laterality refers to the preferred use of either left or right limbs or organs to perform a specific task. We investigated motor laterality in goats (Capra hircus), using the First-stepping Task. During this task, the first foreleg used to step off a board after standing with both forelimbs was recorded. Subjects varied individually in their expression of motor laterization with 36.6% of subjects showing individual-level asymmetries. However, goats as a group did not show a preference for a specific foreleg or lateralization in general. Our results support the hypothesis that the need to coordinate behaviour among conspecifics might be important for determining the presence of laterization at the population level. We suggest that future research investigates how social complexity might affect population-level asymmetries, and whether stimuli with high emotional valence impact on laterization presence and level (i.e., individual or population).

ARTICLE HISTORY

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KEYWORDS Capra hircus; lateral bias; laterality; lateralization; ungulates

Introduction

Behavioural laterization consists of perceptual and motor lateralization and is a common adaptation shared by both vertebrates and invertebrates (Rogers & Vallortigara, 2015). This adaptation has been favoured by evolution because it increases neural capacity and therefore cognitive performance (Rogers, 2014). Moreover, processing specific stimuli with one brain hemisphere allows the other hemisphere to specialise on other functions (Dadda & Bisazza, 2006; Friedlaender et al., 2017; Rogers, Zucca, & Vallortigara, 2004;
Sovrano, Dadda, & Bisazza, 2005). Lateralized animals are thus generally more efficient in performing simultaneous tasks (Rogers & Vallortigara, 2015). For example, chicks (Gallus gallus domesticus) exhibiting visual lateralization detect predators faster and distinguish grain and pebbles easier than non-lateralized chicks, enabling them to feed more efficiently (Rogers, 2000; 2014). Although lateralization is generally advantageous, disadvantages may arise in cases of population-level asymmetries. Prey escape direction, for example, can depend on lateralization bias (Ghirlanda, Frasnelli, & Vallortigara, 2009). When there is a population alignment of lateralization, predators may adapt for hunting prey escaping in a specific direction or that are slower at spotting predators with their left or right eye, making the majority of the prey population easier to catch (Ghirlanda & Vallortigara, 2004; Vallortigara, 2006). However, Ghirlanda and Vallortigara (2004) suggest that intraspecific coordination presents more advantages than the disadvantages caused by behavioural predictability so that lateralization alignments at the population level are mainly found in group-living species.

Motor laterality refers to the preferential use of a limb or organ to accomplish specific tasks (Ströckens, Güntürkün, & Ocklenburg, 2013). Different tests have been developed to assess functional motor asymmetries. For example, a preferred limb used to reach food or to remove a small piece of tape from the eye or nose is found in dogs (Canis lupus familiaris; Aydınoğlu et al., 2000; Quaranta, Siniscalchi, & Vallortigara, 2007; Quaranta, Siniscalchi, Frate, & Vallortigara, 2004). Also, the standing position of the forelimb is generally recorded in ungulates as an indicator for their preferred limb side (McGreevy & Rogers, 2005; Zucca, Cerri, Carluccio, & Baciadonna, 2011). The First-stepping Task has recently been developed to assess asymmetry in domestic ungulates (Tomkins, Thomson, & McGreevy, 2010; Versace, Morgante, Pulina, & Vallortigara, 2007). In this test, the animal is required to step off or on a platform from a standing position (both forelimbs kept in parallel position). The first limb moved forward to step off or on the platform is then recorded. This test is preferred to other methods because it is not influenced by several individual factors, such as the motivational states of the animals, their age or sex (Tomkins et al., 2010).

Hemispheric asymmetries can be used as indicators for affective states because the right hemisphere has a primary role in processing stress and pain (Rogers, 2010; Zucca, Baciadonna, Masci, & Mariscoli, 2011). As such, hemispheric asymmetries might be used as an important indicator of animal emotional states for implementing issues related to animal welfare, especially in farmed animals (Leliveld, Langbein, & Puppe, 2013). To date, among farm livestock, behavioural asymmetries have been mainly studied in chickens (e.g., Daisley, Mascalzoni, Rosa-Salva, Rugani, & Regolin, 2009; Deng & Rogers, 2002; Rogers, 2000), cattle (Bos taurus; e.g., Forsberg, Pettersson, Ljungberg, & Svennersten-Sjaunja, 2008; Rizhova & Kokorina, 2005; Zejdová, Falta, Chládek, & Máchal, 2014) and sheep (Ovis aries; e.g., Barnard,
We investigated whether domestic goats present an asymmetry in using their left or right forelimb descending from an obstacle. To this aim, we assessed the presence of individual-level and population-level motor asymmetries in the use of the forelimb using the First-stepping Task (Tomkins et al., 2010).

**Methods**

**Subjects and management conditions**

The study was carried out at a goat sanctuary (Buttercups Sanctuary for Goats, http://www.buttercups.org.uk; Kent, UK). Goats were habituated to human presence and handling because daily routine care for the animals was provided by employees, volunteers, and researchers. During daytime, goats were placed into two open fields that had shelters. During night time, goats were moved indoors in individual or shared pens (average size = 3.5 m²) with straw bedding. Goats had *ad libitum* access to hay, grass, and water. The animals were also fed with a commercial concentrate in quantities that vary according to their state and age. Thirty subjects, 13 females and 17 castrated males, of different breeds and ages (age range: 2–16 years old) were tested from September to October 2015.

**Test procedure**

A rectangular pen (7 m × 1.70 m) was set up in one of the fields that is part of the goats’ normal daytime area so that the tested subjects had visual and acoustic contacts with conspecifics. A wooden platform (1.17 m × 2.80 m, height 0.2 m) was placed in the middle of the long side of the pen. During testing, the experimenter led a test subject on the platform and held it on a leash (length: 1.8 m) using both hands (Tomkins et al., 2010). When the goat stood square, i.e., with both forelimb in parallel and no tension on the leash (Figure 1), the experimenter threw a small piece of dry pasta on the ground straight ahead of the subject to encourage it to step off from the wooden platform. The first limb lifted by the goat to step off from the platform was recorded. The procedure was repeated 30 times for each goat on the same day. With 50% of the test subjects, the experimenter stood and held the subject on the right side during the first 15 trials and changed position to the left side for the remaining 15 trials. The other 50% of subjects received the reversed order. The position of the researcher (left or right side of the goat) was counterbalanced between subjects to avoid any influence of the side of the experimenter on the limb used to step off from the platform.
Laterality measures

We calculated a laterality index (LI) for each goat \((R - L)/R + L\) to assess the strength of limb preference use on the population level. A LI score of 1.0 represents the exclusive use of the left limb and a LI score of \(-1.0\) corresponds to the exclusive use of the right limb. A LI score of 0 indicates the equal use of the L and R limbs. The limb choices (left or right) of the 30 trials were also used to calculate a binomial \(z\)-score for each subject determining if the use of the right or left limb differed significantly from what would be expected based on a random choice of the left or right limb. The formula used to calculate the score was \(z = (R - 0.5N)/\sqrt{0.25N}\), where \(R\) equals the number of right limb uses and \(N\) indicates the sum of right plus left limb uses. Subjects with a positive \(z\)-score value \(\geq 1.96\) were considered to use mainly the right limb, while those with a negative \(z\)-score value \(\leq -1.96\) were considered to use mainly the left limb (Siniscalchi, Quaranta, & Rogers, 2008). Subjects between both values were classified as ambilateral (A).

Statistical analysis

Chi-square test was used to determine if a significant majority of the subjects was lateralized. In order to test whether goats were lateralized, we first compared the number of L- and R-individuals with the number of A-individuals. The distribution of limb preferences at the population level (i.e., LI) was tested with a one-sample \(t\)-test against the absence of laterality (0.5). The LI calculated when the experimenter was on the left side of the goats was...

Figure 1. Arena used during the First-stepping test. The first foreleg lifted by the goat to step off the platform was recorded.
compared with the LI calculated when the experimenter was on the right side using a paired-sample $t$-test. Differences in laterality indices between males and females were tested with an independent-sample $t$-test.

**Ethical note**

Animal care and all experimental procedures were conducted in accordance with the Association for the Study of Animal Behaviour (Association for the Study of Animal Behaviour, 2017) guidelines. The study was approved by the Animal Welfare and Ethical Review Board of Queen Mary University of London (002/2016AWERBqmul). The tests were non-invasive and behaviours indicating stress were monitored. None of the goats displayed signs of stress during the study.

**Results**

The limb used to step off from the wooden platform, the individual LI and binomial $z$-score are reported in Table 1. Six goats (20%) preferentially used the right limb and five goats (16.6%) preferentially used the left forelimb to step off from the wooden platform. The remaining 19 goats (63.3%) were classified as ambilateral (no limb preference). The number of lateralized and non-lateralized subjects did not differ at the population level (Chi-square test: $p = 0.144$). The distribution of the limb preference was not significantly different from that expected by chance (one-sample $t$-test: $t(29) = −0.018$, $p = 0.98$). The position of the experimenter during the test did not affect the use of the limb in stepping off the platform (paired-sample $t$-test: $t(29) = −0.85$, $p = 0.39$). Similarly, limb preference in males and females was not significantly different (independent-sample $t$-test: $t(28) = −0.64$, $p = 0.83$).

**Discussion**

We assessed the limb preference of goats at the individual and population level during a First-stepping Task. At the individual level, 11/30 goats preferred to use the left or right leg to step off a platform, but we found no evidence for a general motor asymmetry at the population level. We also did not find evidence for any direction (left or right) of lateralization on the population level either, as well as no sex and age effects. To date, findings on motor asymmetry within and between species appear inconsistent (Ströckens et al., 2013). This inconsistency has been attributed to the different types of assessment methods used (e.g., preferred leg used to start moving, or stepping on or off an obstacle; McGreevy & Rogers, 2005; Langbein, 2012; Ströckens et al., 2013; Tomkins et al., 2010; Versace et al., 2007). This indicates the need to further validate the reliability of these methods to test motor asymmetries.
The use of the first forelimb to be moved in this task does not imply coordination among individuals and this might also explain the absence of population-level asymmetries, as hypothesized by Ghirlanda and Vallortigara (2004). For example, one-day-old lambs and adult sheep do not show asymmetries at the population level when performing spontaneous motor behaviours (e.g., stepping forward, standing position, laying and movements of the tail during the suckling; Lane & Phillips, 2004; Versace et al., 2007). However, adult sheep exhibit right-side biases when facing an obstacle before being reunited with a conspecific (Versace et al., 2007). It has also been suggested that some inconsistencies on different findings on anatomical asymmetry (e.g., use of preferred limb) might be explained best by the different types of tasks used to assess motor asymmetries (Rogers, 2010; Tomkins et al., 2010).

Ecological factors can also provide alternative explanations for our results. For example, moving in difficult mountainous terrain may have resulted in goats having no overall preferences for the use of left or right forelegs (Biancardi & Minetti, 2017).

<table>
<thead>
<tr>
<th>Subject</th>
<th>Right forelimb</th>
<th>Left forelimb</th>
<th>LI</th>
<th>Binomial z-score</th>
<th>Classification</th>
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<tr>
<td>1</td>
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<td>1.09</td>
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<tr>
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<td>0.40</td>
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</tr>
<tr>
<td>4</td>
<td>20</td>
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<td>0.33</td>
<td>1.82</td>
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<tr>
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<tr>
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Gaining a better understanding of the relationship between motor latera-
lization and emotional stimuli has the potential to improve animal welfare
(Leliveld et al., 2013). Specific behaviours (e.g., the preferred use of the left
or right eye or the position of the head while listening to different sounds)
can indicate how external emotional stimuli are perceived and processed dif-
fferently by the two hemispheres of the brain depending on their correspond-
ing valence and familiarity (Rogers & Andrew, 2002). For example, conspecific
sound stimuli elicit a different lateralized response than heterospecific ones.
Horses show a right bias (left hemisphere processing) for calls emitted from
a familiar neighbour (familiar horse housed in a close field or stall) but no pre-
ference for other group members or strangers (Basile et al., 2009). In dogs, a
left head orienting bias is related to the vocalisations encoding intense
emotions, regardless of their valence (i.e., isolation, disturbance mainly nega-
tive and play mainly positive; Siniscalchi et al., 2008). Recent research has
shown that dogs also exhibit a right hemisphere asymmetry (left head orient-
ing bias) in response to a meaningless human voice (phonemic components
removed) with positive intonation (Ratcliffe & Reby, 2014).

Hemispheric asymmetries can be additionally affected by personality type,
environmental conditions, sex and domestication (Rogers, 2010; Zucca, Cerri,
et al., 2011). The use of one limb and personality type can potentially predict
responses to novel situations of an individual (Rogers, 2010). For example,
chimpanzees (Pan troglodytes) and marmosets (Callithrix jacchus) with a left-
hand preference in holding and collecting food are more likely to approach
a novel object (Cameron & Rogers, 1999; Hopkins & Bennett, 1994). Left-
handed marmosets are also reported to receive more conspecific aggression
(Gordon & Rogers, 2015). In dogs, a lack of asymmetry in the use of the limbs is
associated with strong reactions to fearful stimuli (e.g., thunderstorm and fire-
works; Branson & Rogers, 2006). Domestication and human handling can also
influence lateralization. For example, young feral horses (Equus caballus) have
been found to show strong individual right-forelimb preferences but feral
horses as a group did not show motor lateralization at the population level
(Austin & Rogers, 2012). The authors suggest that motor lateralization pre-
viously reported in domestic horses might be caused by human interactions,
deeming motor lateralization unreliable as a measure of lateralization in
horses. However, motor lateralization has been documented in wild ungulates
(e.g., ibex, Capra ibex; Sarasa, Soriguer, Serrano, Granados, & Perez, 2014; elk,
Cervus canadensis; Found & Clair, 2017), indicating that human interaction is
not a necessary factor for motor lateralization in ungulates. Knowledge
about which side animals are more reactive can provide valuable indications
on how to approach them and ultimately handling them more efficiently
(Austin & Rogers, 2007; McGreevy & Rogers, 2005). Environmental conditions
can also determine changes in hemispheric control, as shown by the presence
of asymmetry associated with the development of negative cognitive biases
(i.e., negative perception of ambiguous stimuli). Specifically, these biases seem to be related to the predominance of the right hemisphere, which is usually implicated in processing negative emotions and behavioural avoidance (Baciadonna & McElligott, 2015; Rogers, 2010). Wells, Hepper, Milligan, and Barnard (2017) showed that ambilateral and right-pawed dogs approached food bowls increasingly slower the further it was located from a baited position. By contrast, left-pawed individuals approached food bowls at approximately the same speed not considering the distance of the food bowls from the baited position so that they displayed a more pessimistic outlook than the other tested dogs.

In conclusion, goats did not show asymmetries at the population level in a First-stepping Test. Our results thus support the hypothesis that population-level asymmetries are more likely to occur in tasks that require social coordination among behaviourally asymmetric individuals. Future research should address the effects of social behaviours on brain asymmetries. Moreover, further knowledge on presence/absence of lateralization in stressful conditions might be also useful to predict animal behaviours and enhance their living condition because individual-lateralized behavioural responses indicate how animals process environmental stimuli.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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