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Short report

Space availability influence laterality in donkeys (*Equus asinus*)

Paolo Zucca[a,*], Francesco Cerri[b], Augusto Carluccio[c], Luigi Baciadonna[d]

[a] *Zooantropology Unit, Healthcare Services Agency 1, Loc. Prosecco Stazione, 20, 34010 Sgonico, Trieste, Italy*
[b] *Centre for Mind/Brain Sciences, University of Trento, Italy*
[c] *Department of Veterinary Clinical Sciences, University of Teramo, Italy*
[d] *Department of Relational Sciences, University of Naples "Federico II", Italy*

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ABSTRACT

Cerebral lateralization is the portioning of the cognitive functions between the two cerebral hemispheres. Several factors, like embryological manipulations, light exposure, health conditions, sex and age can influence the left–right brain asymmetries and contribute to increasing the variability in the strength and direction of laterality within most species. We investigated the influence of an environmental constraint, namely space availability, as a new source of variation on laterality in an adult vertebrate model, the donkey. In a baseline condition we tested whether donkeys show a motor lateralization bias at population level, while in an experimental condition we manipulated space availability to verify if a reduction in this parameter could represent a new source of variation in laterality. Results show that donkeys are lateralized at population level with a strong bias to standing with the right forelimb advanced over the left and that a reduction of space availability is an important source of variation in the laterality strength and direction within this species. The comparative analysis of the environmental and developmental factors that give origin to neural and behavioural laterality in animal models will be very important for a better understanding of the evolutionary origin of such multifaceted phenomenon.

1. Introduction

Cerebral lateralization is an evolutionarily ancient adaptation that has been demonstrated in several vertebrates and invertebrate taxa. The left hemisphere, which primarily processes input from the right eye, controls responses that require considered discrimination between stimuli and for control of motor responses involving object manipulation; the right hemisphere controls rapid, species-typical responses, expresses intense emotions and controls visuo-spatial processes centred on relational properties of the spatial layout (Andrew and Rogers, 2002; Vallortigara and Rogers, 2005). There is considerable evidence supporting the idea that lateralized brains are more efficient in terms of cognition and fitness (Rogers et al., 2004; Vallortigara et al., 2011) and one model, proposed by Ghirlanda and Vallortigara (2004), seem to explain within-species variation in the direction and the strength of lateralization. Strategic factors that arise from the balance between competitive and cooperative interactions can explain by themselves the phylogenies of lateralization as an evolutionary stable strategy (Ghirlanda et al., 2009).

However, there are several other factors that can influence the left–right asymmetries and can contribute to increasing the variability in the strength and direction of laterality within most species (Reddon and Hurd, 2008). Rogers (1990) demonstrated that it is possible to manipulate the direction of lateralization in chicks by exposing the eggs to light for a brief period during the last 3 days before hatching. Sex is another important factor affecting the strength of lateralization (Bianki and Filippova, 2001; Tommasi and Vallortigara, 2004; Reddon and Hurd, 2008); health conditions strongly influence the strength of laterality bias between healthy and sick lions (Zucca et al., 2010). Individual differences in aggressiveness and personality-like behavioural traits in a cichlid fish (Reddon and Hurd, 2008) and horse breeds (McGreevy and Thomson, 2006) have been described as sources of variation in laterality. Another factor influencing the direction of lateralization is age. In fact, primates and other species of monkeys exhibit age-related differences in the strength and direction of hand preference in tasks that involve the use of tools (Ward et al., 1990); horses show the effect of age on their forelimb preference when standing in a quadrupedal position (McGreevy and Rogers, 2005) and hamsters show an ontogenetic decrease in lateralization strength during development (Uziel et al., 1998). Training and handling procedures represent another source of variation in left–right asymmetries. In fact, the convention that donkeys, like horses, are handled mainly from the left side may have an effect on the strength and the direction of laterality in adult trained animals (McGreevy and Rogers, 2005). Horses show a stronger escape turning behaviour when a novel stimulus is presented on

* Corresponding author. Tel.: +39 040 251283; fax: +39 040 251310.
E-mail address: zucca@units.it (P. Zucca).

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the left side (Austin and Rogers, 2007) while the emotional status of horses exposed to novel situation influences the lateralization bias in visual behaviour (Larose et al., 2006). The effect of experience seems to play a role in the paw preference also in rats (Tang and Verstynen, 2002).

Another potential source of variation in laterality, which has received little attention, is the effect of environmental constraints, such as space availability, in adult animal models. The present research investigates whether space availability could influence the direction and strength of laterality in adult donkeys (*Equus asinus*). In the baseline condition we tested whether donkeys show a laterality bias at population level by observing the position of the forelimb in relation to one another while standing. We then manipulated the space availability, predicting that the reduction of space should affect the strength and the direction of laterality (left–right asymmetries) at population level.

2. Material and methods

2.1. Subjects

Nineteen adult domestic donkeys, housed at the experimental farm of Teramo University, participated in this study. Of the 19 subjects, there were 10 males and 9 females of different ages (from 2 to 16 years old), and they were kept at the University facilities only for genetic purposes. The cut-off value for dividing the sample group of animals into young and old subjects was 6 years old and age groups were counterbalanced for sex as follows: females, 4 young and 5 old; males, 5 young and 5 old. We specifically selected unhandled subjects to avoid any interference of training procedures on laterality.

2.2. Procedure

During the baseline condition ("large paddock"), the two groups of donkeys were observed in their two residential paddocks of the same size (approximately 600 m^2). The position of the foreleg while standing in relation to one another was recorded, and the sampling was made when the donkey maintained the quadrupedal standing position for at least 5 s, to yield 30 observations for each subject. Observations were made from the side of the donkeys to ensure accurate recording of the forelimb position and to avoid parallax errors, according to the protocol suggested by McGreevy and Rogers (2005) and the sampling of each donkey was completed in one session that took about 30–45 min each. The standing behaviour was sub-divided into standing with the left forelimb advanced (SL), standing with the right forelimb advanced (SR) or standing square (SS), i.e. with forelegs level with one another. Each subject was marked to allow individual identification and observations were made from the side of the donkeys to ensure accurate recording of the forelimb position and to avoid parallax errors, as suggested by Larose et al. (2006). The baseline condition did not involve any prior handling or moving of the animals from their residential paddocks.

The experimental condition (small paddock) investigated the effect of an environmental constraint by means of decreasing the residential space availability. Each group of subjects was moved separately into two smaller and contiguous experimental paddocks that were about half the size of the residential one (see Fig. 1). After 2 days of habituation in the smaller paddocks, each donkey in the two groups was scored again for motor laterality using the same procedure as the baseline condition.

This experiment has been carried out in accordance with the European Communities Council Directive of 24 November 1986 (86/609/EEC) and it complies with the Italian laws on animal research and welfare.

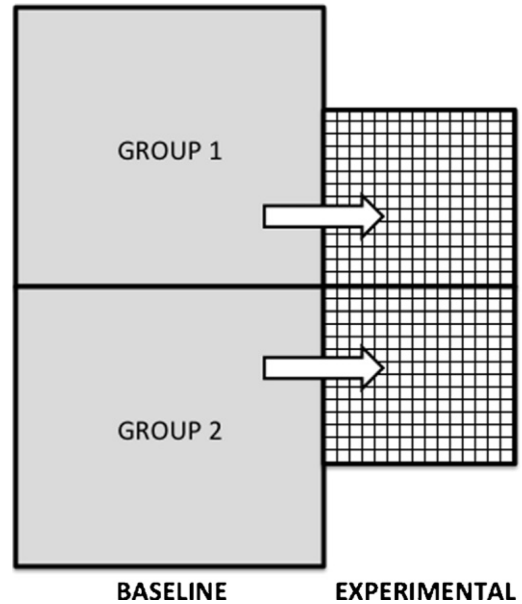

Fig. 1. Schematic representation of the baseline (large) and experimental (small) paddocks; arrows show the communication gates between the baseline and the experimental paddocks.

2.3. Statistical procedures

During the baseline condition, the Laterality Index (LI) of motor preferences for each subject was calculated as $(SR/SR + SL) \times 100$, where SR is the number of times each was observed standing with the right foreleg advanced and SL the number of times the left

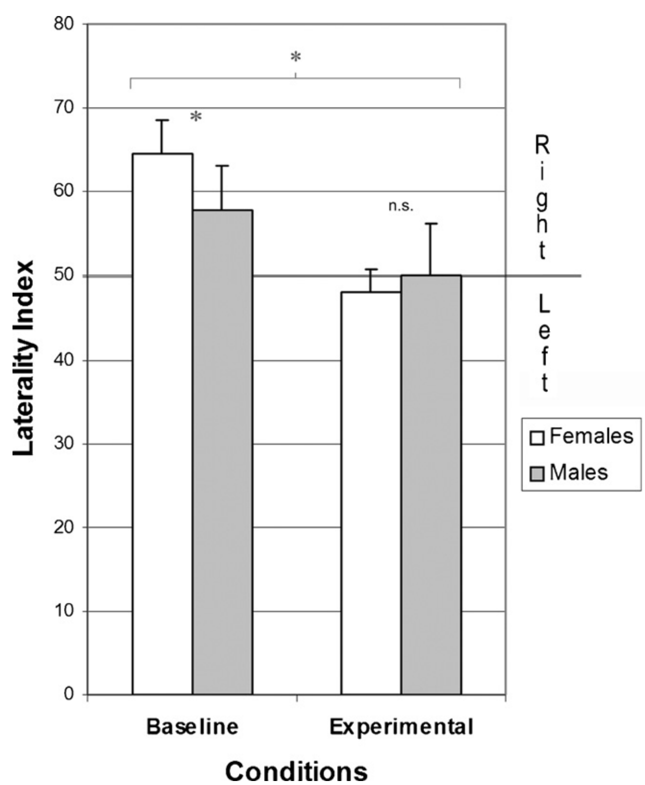

Fig. 2. Average Laterality Index (LI) scores (±s.e.) for females (white bars) and males (grey bars) in the baseline (large) and experimental (small) conditions. There is a significant difference between the LI in the two conditions baseline (large)/experimental (small) and the laterality bias at population level disappears when animals experience a space reduction in the experimental condition.