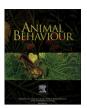
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Novelty affects paw preference performance in adult mice

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Keywords: brain asymmetry consistency of laterality habituation pawedness The hemispheres are asymmetrically involved in the reaction to stressful situations. In this sense, it is possible to speculate that the asymmetrical activation of the hemispheres, as a result of the exposure to a novel situation, may affect behavioural lateralization. We tested the hypothesis that novelty affects performance in a paw preference task in 37 habituated (HAB) and 37 control (CT) adult male Swiss mice. For 4 days prior to the first testing session, HAB mice were placed in the testing box daily. After the fourth session, animals were deprived of food for 24 h. On the 5th day, food pellets were placed inside a feeding tube and animals were allowed to make 25 successful retrievals of food pellets. The testing procedure was repeated 4 days later. CT mice were not submitted to the habituation sessions. A significant sidedependent difference in consistency of laterality was observed between groups in the first session: all (100%) right-pawed CT mice used their right paw to make their first successful retrieval of food in the first testing session, while only 61% of left-pawed mice used their left paw. The same pattern was observed when the first five retrievals were considered: 100% right-pawed CT mice and 72% left-pawed CT mice were consistent. No differences were observed in the HAB group; in both side-preference subgroups, 88% of the animals showed consistent laterality. These results indicate that behavioural lateralization in paw preference is affected by the novelty of the testing situation in a side-dependent manner.

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One of the most prominent features of behavioural lateralization in humans is the fact that the vast majority (approximately 90%) of the population consistently uses the right hand in tasks such as writing and drawing (Annett 2002). In spite of the fact that a considerable effort has been made in trying to assess the neurobiological basis of this remarkable behavioural trait, a comprehensive description of the mechanisms that determine human hand preference in particular and behavioural lateralization in general is not yet possible. Currently, it is believed that behavioural lateralization is the observable expression of functional specializations of the brain hemispheres (Rogers 2009). In turn, the functional specializations that have been uncovered so far, such as those related to language and attention, are thought to reflect biochemical and/or structural differences between the hemispheres (Hellige et al. 1998; Mesulam 1999; Josse & Tzourio-Mazoyer 2004).

In trying to explain how asymmetrical hemispheres coordinate their functions during the execution of lateralized behaviours, both

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animal models and humans have been studied (Vallortigara & Rogers 2005). Interestingly, some studies have shown that patterns of hemispheric lateralization change with practise (Castellano et al. 1989), even over the course of a single experiment (Streitfeld 1985; Burton & Wilson 1990; Fagot & Vauclair 1991, 1994; Van Horn et al. 1998). Shifts from an initial right-hemisphere advantage in early trials towards left-hemisphere advantage in later ones have been described with auditory (Burton & Wilson 1990), visual (Streitfeld 1985) and tactile (Streitfeld 1985) stimuli. In a similar way, nonhuman primates tested in somatosensory discrimination tasks presented a reduction of their initial predominance of left hand preferences with practise (Ettlinger & Moffett 1964; Brown & Ettlinger 1983). In toads (Robins & Rogers 2006), the left visual hemifield is preferentially used to observe and attack complex prey stimuli identified as novel. This left visual hemifield advantage disappeared with repeated testing. Interestingly, in these animals, predatory responses directed at familiar prey are usually carried out using the right visual hemifield. A similar shift in preference has also been observed for lizards (Robins et al. 2005). These results support the idea that the right hemisphere is specialized for the processing of new tasks, having an important role in the initial phases of acquisition, while the left hemisphere plays a major role in tasks for which the individual already has some training. Therefore, right-to-left shifts should be

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expected after some practise. The theory also points to the possibility that shifts in lateralization at the population level that accompany practise reflect changes in lateralization in a subset of individuals: those for whom an initial advantage of the right hemisphere was observed (Kittler et al. 1989). Given the natural limitations that are present in primate studies, the existence of behavioural lateralization and functional specialization in other species allows for the systematic study of factors that may be implicated in the expression of these traits (Corballis 2009).

Skilled reaching, as exemplified by forelimb use, has been identified in many species (Rogers 2009). Of particular interest to the present study is the fact that, in some of these species, individuals show a marked and consistent preference towards the use of one of the hands/paws. Despite the fact that hand/paw preference in animal models may not constitute a clear homologue, or even an analogue, of human hand preference, it can be used to assess the mechanisms underlying behavioural lateralization, providing evidence that may be used in understanding human lateralization (Rogers 2009), including hand preference.

One of the most frequently used tests to assess pawedness in rodents, developed by Collins (1968, 1969), intrinsically involves exposure to a novel situation. In this test, after a period of food deprivation, mice are removed from their home cage and individually placed in a small testing box where they are required to perform a reaching task in order to retrieve small quantities of food that are made available in a feeding tube. In spite of its frequent use as an investigative tool, little is known about the possible effects that the novel, and potentially anxiogenic, situation has on overall performance during the test, including parameters such as degree and consistency of lateralization. Several studies demonstrated that the Collins's paw preference test has a high intertest consistency of results regarding magnitude and direction of lateralization (Schmidt et al. 1991; Manhães et al. 2003, 2005). Much higher than the intertest reliability observed for other frequently used tests of behavioural lateralization in rodents such as the free-swimming and tail-suspension tests (Schmidt et al. 1999; Filgueiras & Manhães 2004, 2005; Manhães et al. 2007). This high reliability would seem to indicate that the patterns of lateralization observed in the paw preference test are not affected by factors such as the novelty of the testing situation. However, there are some indications that this might not be the case. For instance, it has been demonstrated that practise increases the magnitude of lateralization in several tests that assess behavioural lateralization (Castellano et al. 1989), including the Collins's test (Bulman-Fleming et al. 1997). These results suggest that a learning process may be relevant to consolidate lateralization in tests that are heavily dependent on the animal's ability to acquire new behaviours while dealing with novel situations. Furthermore, evidence is available indicating that the hemispheres are asymmetrically involved in the rodent's reaction to stressful situations (Krahe et al. 2002; Filgueiras et al. 2006). In this sense, it is possible to speculate that the asymmetrical activation of the hemispheres as a result of the exposure to a novel situation may affect the initial selection of the paw to be used in retrieving the food in the Collins's paw preference test and, as a result of a learning process, this initial choice would be readily consolidated, leading to a stable lateralization.

One way to ascertain the effects of novelty on paw preference performance is to compare animals that were previously habituated to their testing environment (Leussis & Bolivar 2006) with animals that were not exposed to that environment prior to the paw preference task. Therefore, in the present study, we analysed the effects of novelty on performance and consistency of laterality in a paw preference task using a test adapted (Schmidt et al. 1991; Manhães et al. 1993, 2003, 2005) from a procedure initially described by Collins (1968, 1969).

METHODS

Subjects

Subjects were 74 (21 litters) adult Swiss male mice that were randomly assigned into two groups: habituated (HAB: N=37) and control (CT: N=37). All mice were bred and maintained in our laboratory in the same conditions without interventions during the first 21 postnatal days. The animals were kept in a temperature-controlled room on a 12 h light:dark cycle. Access to food and water was ad libitum (except when otherwise specified). All experiments were conducted in accordance with the declaration of Helsinki and with the Guide for the Care and Use of Laboratory Animals as adopted and promulgated by the National Institutes of Health (U.S.A.). The experiments were conducted to minimize the number of animals used and the suffering caused by the procedures used in the present study.

Testing Procedure

Paw preference test began at adulthood (3 months). For the habituated group, the first test was preceded by a habituation period of 4 days in which the animals were individually placed in the paw preference testing box (7.5 \times 7.5 \times 14.0 cm, W \times L \times H) for 15 min at a time, once a day. The box had a transparent front wall with a cylindrical feeding tube attached to it in an equidistant position from the two side walls (Schmidt et al. 1991; Manhães et al. 1993, 2003, 2005). During this period, the animals had unrestricted access to food in their cages but no food was available in the feeding tube. After leaving the box on the last day of the habituation procedure, animals were deprived of food for 24 h. On the 5th day, animals were once more placed in the testing box to begin the first paw preference testing session. This time, however, the feeding tube was kept empty only during the first 5 min of the testing session, a period that allowed the initial exploratory activity to subside. After this period, animals were required to perform a reaching task in order to retrieve food pellets (4-5 mm in diameter) that were made available in the feeding tube. The food pellets were the same that were regularly used to feed the animals, so that all mice were used to the smell, taste and texture of the pellets. Given the placement of the feeding tube, the food could be equally accessed by the right or the left paw. Therefore, left or right paw reaches could be easily observed. Every behavioural session consisted of 25 reaches for food. Four days later, animals were again deprived of food for 24 h. Then, animals were placed in the testing box to begin the second testing session, which followed the same procedure described for the first session. In the second session, the experimenters were blind as to the scores previously obtained in the first session. Control (CT) mice were not subjected to the 4-day habituation period prior to food deprivation, and food was made available in the feeding tube immediately after the animals were placed in the testing box. All testing sessions were videotaped and the experimenter only started recording when the first pellet was placed in the feeding tube. These recordings were subsequently used to assess paw preference performance.

Laterality

We performed the analysis of laterality using procedures described in previous reports (Schmidt et al. 1991; Manhães et al. 1993, 2003, 2005). Briefly, we noted the paw that was used to remove the pellet from the feeding tube. For each animal, the percentage of left paw use (%L = number of left paw reaches in both sessions \times 100/50) was used to evaluate side preference and the percentage of preferred paw use (%PP = number of reaches with

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