Lateralization in the predatory behaviour of the common wall lizard (*Podarcis muralis*)

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ABSTRACT

Ectotherms have been shown being lateralized as well as mammals and birds. This is particularly evident in visual lateralization, i.e. the different use of the eyes, leading to use a specific eye to observe specific kind of stimuli and to process them with the correspondent contralateral hemisphere. Several lower vertebrates are facilitated in this from the lateral position of the eyes, enabling them to carry out more tasks simultaneously, controlled by different eyes and relative hemispheres. Predatory responses seem usually mediated by the right eye/left hemisphere in fishes, amphibians and some sauropsids, but there are no strong evidences of this in lizards. Eighteen wild males of the Common wall lizard *Podarcis muralis* were tested individually in captivity to ascertain whether they are lateralized to look at prey with a specific eye. The lizards were gently induced entering a 30-cm long central arm of a T-maze which led to a 44.5-cm long arm cross-arm at whose extremities there were two identical prey, *Tenebrio molitor* larvae, familiar to the lizards. We recorded what direction the lizards chose to reach the prey and the frequency and duration of head turning, indicative of looking either prey with the left or the right eye. We found that individuals show being lateralized at individual level. The preferred direction taken to reach the prey is the right for the majority of those (4 of 5) showing an evident preference, indicating also a possible form of laterality at population level. In addition, lizards maintained the same head side of the direction taken turned for more time towards the prey than the opposite head side, revealing an eye preference for observing this kind of cue. Our study demonstrates how males of *Podarcis muralis* have a visual lateralization to capture prey. Furthermore, it is another support to the hypothesis of vertebrate lateralization derivation from a common ancestor.

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1. Introduction

Cerebral lateralization, i.e. the preferential use of one side of the body as a consequence of hemispherical specialization to control specific functions, has been studied in many mammals and birds, and in the past three decades in lower vertebrates too. The presence of lateralization in ectotherms, in fact, indicates that it is the expression of anatomical and consequent behavioural asymmetries. Thus, it is likely not the result of an evolutionary convergence, but a plesiomorphic character (e.g. Vallortigara and Bisazza, 2002). Many studies (e.g. Andrew, 1983; Rogers et al., 1985; Andrew and Dharmaretnam, 1993) have taken into consideration the likelihood that lateral-eyed animals, as are many ectotherms, are able to perform different tasks in response to a visual stimulus coming from either their left- or right-hand side. These animals also prefer to

look at particular stimuli with either their left or their right eye, then process the stimuli with the contralateral hemisphere. As far as we know, this kind of visual asymmetry is effectively widespread among lateral-eyed ectotherms (Vallortigara et al., 1999a).

Independent eye use when observing the environment may lead to different brain elaboration of cues coming from different visual hemifields simultaneously. This allows the brain to avoid neuronal competition in the response to the stimuli, making the lateralization an efficient evolutionary solution for "functional incompatibility" (Sherry and Schachter, 1987).

Lizards are very interesting subjects in the study of lateralization, as the lateral position of their eyes minimizes binocular view and, similarly to other ectotherms, they do not have a large corpus callosum, which allows connection and communication between the two hemispheres. This is the case, for example, of *Iguana iguana*, where these connections are minimal (Butler and Northcutt, 1971). In *Anolis* lizards the visual system produces a hemisphere which is somewhat 'unaware' of what the other perceives, as a whole working as a "split brain" (Deckel, 1995). In anoles (*Anolis carolinensis*),

and in male tree lizards (*Urosaurus ornatus*), aggression shows a left eye bias (Deckel, 1995; Hews and Worthington, 2001); in *Sceloporus virgatus* such phenomenon occurs in females too (Hews et al., 2004). Such a direction of lateralization for aggression tasks is widespread in different vertebrate taxa, in ectotherms, as in non-human primates (Vallortigara et al., 1999a; Hews and Worthington, 2001), suggesting that this behaviour is preferentially controlled by the right hemisphere.

A dissimilar situation is found in the predatory context, which seems to be right eye/left hemisphere mediated in several species of toads and bony fishes. In sauropsids our data are limited: we are aware of one study only, concerning a social group of the agamid lizard *Ctenophorus ornatus*, where the right eye (left hemisphere) preference to control the predatory response seems to become stronger with familiarization to the prey (Robins et al., 2005). The habituation to the prey, therefore, could be important for the direction of visual lateralization, affecting the predatory cue codification. This reveals that there may exist an association between direction bias and experience, proving a complementary reptile brain specialization for processing different visual stimuli perceived from the close environment (Robins et al., 2005).

We aimed at ascertaining the possible existence of visual lateralization forms in the lacertid lizard *Podarcis muralis* in the predatory context. Our goal was to discover whether, when the lizard perceives two familiar prey with both eyes simultaneously in the monocular lateral field, it shows a preferential lateral direction, thus revealing a form of lateralization, and if this can be assessed at individual or population level, or both. We supposed that *Podarcis muralis* lizards, similarly to other ectotherms, are lateralized in the predatory response control, and we therefore expected a right eye/left hemisphere preference when observing the prey.

2. Materials and methods

From April to September 2007 we collected 18 adult male *Podarcis muralis* lizards from scattered small populations in Parma. They were captured by noose, a harmless and widespread capture method. They were then put in cloth bags and carried to the laboratory, where they were housed individually in 60 cm × 50 cm × 50 cm wood terraria. They had the front and one lateral side in glass, a 2 mm × 2 mm wire mesh ceiling, floor covered with sand, one pebble and one brick for refuge and/or basking site; water was provided *ad libitum*. The terraria were located in a previous greenhouse, with full glass sides, but opaque roof; light, photoperiod and temperature were therefore natural, although artificial light and heat could be provided if necessary.

Once entering the terrarium, the lizards were fed with mealworm larvae (*Tenebrio molitor*), dusted with multivitamin powder. Here they remained for 1 week at least, being fed at 2–3 day intervals to accustom to the new environment and the food. This period was followed by 3 days of fasting before the tests (McKeehan and Sievert, 1996; Cooper, 2000; Shine, 2003) to induce and equalise the predatory motivation. At the end of each test-day the lizards were fed with one mealworm larva. The test sequence protocol lasted about 15 days and the lizards, therefore, remained in captivity for 3 weeks. At the end of the experimental period they were released at the same site of capture. None of them was harmed by the experiment, which was carried out under licence from Italian authorities.

The experimental apparatus consisted of one 8 cm × 30 cm × 6 cm and 8 cm × 44.5 cm × 6 cm PVC T-maze, covered with transparent and colourless plexiglas strips. The central arm of the maze had a rear entrance for the lizard, while the opposite end was the entrance to the cross-arm, which was prevented by a sliding sluice-gate, remotely operated by the observer by a cable. The cross-arm of the maze had one prey at both ends. The access to this arm of the maze was limited by two restriction blocks, which reduced the passage width to 4 cm, to force the lizard having a straight head when entering the arm and then having the opportunity to see both prey with either eye at the same time, even though they might possess an even limited frontal binocular vision. This was to avoid that the lizard could choose either prey because seeing it first and then avoiding that the preference was not due to a form of lateralization. Light was homogeneous for the whole experimental apparatus and came from direct sunshine.

As prey we used two mealworm larvae (*Tenebrio molitor*), then already known to the lizards at testing. Not to influence the choice, we selected two identical prey by measuring their size putting them on graph paper and then freezing them, to avoid that their different movements could affect the lizard's choice. The position of the larvae was reversed after every test. A colourless, transparent plexiglas barrier before the prey prevented the lizard from ingesting the mealworm at the end of the test, in order to avoid that feeding could affect the motivation to prey in next test. Two new larvae were used at the beginning of each test-day.

At testing each individual was gently forced to enter the central arm of the maze, which was then closed. Here they remained for 15 min. The test started when the sluice-gate was lifted up and ended when the lizard reached either prey, whereas it was considered void if the lizard refused to approach either prey within 20 min. The test was recorded with a 2.5 cm × 3.5 cm black and white video camera placed centrally in front of the maze and videotaped on a digital support. Videos were later reviewed using the "Virtualdub" video programme, which also permitted frame by frame analysis. The lizard behaviour was recorded continuously, using a digital event recorder. We considered the following behaviour parameters and relative occurrence:

- lateral direction chosen after entering the cross-arm of the maze.
- frequency and duration of head position in relation to the longitudinal body axis—right-side head exposure, left-side head turn, centred head position.
- frequency of tongue flicking.
- latency to the first movement.
- latency to enter the cross-arm.
- latency to the first attempt to prey.

Our aim was to repeat the tests 10 times maximum for each individual, with a minimum interval of 60 min between tests; however this was not achieved due to wide individual variation in responsiveness to testing. The maze floor was cleaned with ethylic alcohol before the beginning of every test to remove every chemical cue possibly influencing the subsequent choice. Each lizard was tested three times daily maximum and tested again after 3 days. The number of daily tests could be variable due to meteorological or temperature conditions. Maze floor temperature was measured with a 5.0 cm × 2.2 cm × 1 cm temperature data—logger fixed to the experimental apparatus, with data downloaded with MTT Tempstick software.

We used the Kruskal–Wallis ANOVA (*KW*), to compare durations and tongue-flicking frequency among the individuals, and the Mann–Whitney *U*-test (*U*), to compare the head orientation duration and the final preference, both calculated with the SPSS 14.0 for Windows software (SPSS Inc., 2006). The binomial test was used to ascertain the lateralization at the individual level, whereas the χ^2-component "*z*" index (*z*) (Bishop et al., 1975) to compare the sample's total number of choice for either cross-arm and the tongue-flicking frequency for each side head exposition. Means are listed ±S.E. throughout and the probabil-