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Complementary lateralisation in the exploratory and predatory behaviour of the common wall lizard (*Podarcis muralis*)

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Several ectotherms show lateralisation, particularly visual lateralisation. Such brain specialisation has an ancient origin and is still present in living vertebrates. One important advantage is the possibility for lateralised animals to carry out two tasks at the same time, without altering the efficiency of either one. Recent studies on the common wall lizard (*Podarcis muralis*) found right eye/left hemisphere bias for attention to the cues of prey, and left eye/right hemisphere bias for controlling antipredatory and exploratory behaviours. However, these studies were independent of each other and therefore were not empirical demonstrations that the directions of visual lateralisation found in this species are present in the same individual, allowing the simultaneous performance of dual tasks. In our study the same *Podarcis muralis* individuals carried out one exploratory and one predatory test each. We allowed each lizard to move freely in a circular arena, with opaque walls, with either nothing or mealworm larvae in the centre. In the first case the test was an exploratory test, while in the second case it was a predatory one. The results indicated that lizards preferentially used the left eye to observe the environment—i.e., during exploration—and just tended to use the right eye during predation. Hence we conclude that in the *Podarcis muralis* lizard lateralisation is expressed in the same individual in opposite directions, in accordance with previous observations.

Keywords: Common wall lizard; Exploration; *Podarcis muralis*; Predation; Visual lateralisation.

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Cerebral lateralisation is widespread among animal species. The fact that it is present not only in endotherms but also in ectotherms supports the hypothesis that it was inherited from a common ancestor. This is probably because lateralisation is advantageous (MacNeilage, Rogers, & Vallortigara, 2009; Rogers & Andrew, 2002).

Dharmaretnam and Andrew (1994) observed how different patterns of eye use were evoked by the perception of different stimuli. In fact, different reactions to right- and left-placed stimuli have been ascertained in several species of vertebrates, verifying the ability of the brain to perceive information with the left or right eye and to elaborate it with the contralateral hemisphere, according to the nature of the cue (Dharmaretnam & Andrew, 1994). Several subsequent studies confirmed this, supporting the hypothesis of task- and processing-dependent lateral asymmetry (Vallortigara & Bisazza, 2002). In animals with lateral eyes this is particularly evident. The visual system of birds, sauropsids, and fishes allows each eye to be relatively independent from the other eye in perception (Andrew, 1991; Deckel, 1995; Wallman & Pettigrew, 1985); moreover, there is poor interhemispheric communication. Hence, in this condition the brain side dominance prevents the simultaneous initiation of incompatible stimuli responses (Andrew, 1991; Vallortigara, 2000; Vallortigara & Rogers, 2005).

The direction of visual bias is connected to several daily activities, such as foraging (Rogers, 2000) and vigilance (Brown, Western, & Braithwaite, 2007; Robins & Rogers, 2004), enabling the performance of more than one survival task at the same time, processing each one with a different hemisphere (Dadda & Bisazza, 2006a; Rogers, 2000; Rogers, Zucca, & Vallortigara, 2004). If these tasks competed for the same computational visual resource, the performance of each task could be constrained by the brain's ability in processing (Dadda & Bisazza, 2006a; Dukas, 2004). In fact, several studies on birds (*Columba livia*), fishes (*Cyanocitta cristata*), and spiders (*Schizocosa uetzi*) indicated that paying attention to one activity does not allow sufficient attention to be allocated to other activities (Dukas & Kamil, 2000; Güntürkün et al., 2000; Heberts, 2005). In fact, what is really important is not the direction of lateralisation per se but the fact that two opposite tasks are perceived by the opposite sides of the brain (Vallortigara, Rogers, & Bisazza, 1999).

The common wall lizard *Podarcis muralis* is known to have visual lateralisation. Similarly to other lateral-eyed species, it prefers looking at prey with the right eye (Bonati, Csermely, & Romani, 2008; Csermely, Bonati, & Romani, 2010), whereas it uses the left eye to observe potential predators (Bonati, Csermely, López, & Martín, in press) as well as to explore new environments (Csermely, Bonati, López, & Martín, 2009). Such eye use is in accord with what was previously found in several other vertebrate taxa

(Robins & Rogers, 2004; Sovrano, Rainoldi, Bisazza, & Vallortigara, 1999; MacNeilage et al., 2009; Valenti, Sovrano, Zucca, & Vallortigara, 2003).

In this study, we aimed to record the preferential visual direction of *Podarcis muralis* lizards when tested in both predatory and exploratory contexts. We expected to record a preferential visual direction when performing these behaviours, and to record the use of opposite eyes when watching prey and when exploring; i.e., the right eye for monitoring prey and the left eye for exploration. Such results have already been recorded, but the novelty of our experiment is in demonstrating the opposite use of eyes in the same individual, in contrast to previous studies where the analysis of those contexts were independent of each other and used different individuals.

METHOD AND MATERIALS

From April to August 2009, we collected by noose 68 adult *Podarcis muralis* lizards (37 males and 31 females) from scattered populations within the province of Parma. Once captured, they were put in cloth bags and carried to the laboratory, where they were housed individually in PVC cages (49 × 29 × 25 cm) with a sand substratum and some rocks for hiding and basking. Water was provided *ad libitum*. The cages were located in a greenhouse, with full glass sides and an opaque roof; light, photoperiod, and temperature were therefore natural, although artificial light and heat could be provided if necessary. Once in the laboratory, the lizards were fed at 2–3-day intervals with mealworm larvae (*Tenebrio molitor*) dusted with multivitamin powder.

The test sequence protocol consisted of two different tests carried out on two non-consecutive days; the lizards remained in captivity for 7–10 days in total. In one test, the lizards had to explore an empty circular arena (exploratory test), whereas in the other test the lizards were in the same context but in the presence of a potential prey kept in the centre of the arena itself (predatory test). The test sequence was random. The experimental apparatus consisted of one 50-cm diameter and 14-cm high PVC circular arena without a cover. The wall was painted opaque black to prevent the lizard looking outside the arena. Light was homogeneous for the whole experimental apparatus. The tests were carried out when the air temperature was within the 25–40°C range. At the end of the experimental period, the lizards were released at the same site of capture. None of them was harmed by the experiment, which was carried out under licence from the Italian authorities.

Before the predatory tests, the lizards were fasted for 3 days to induce and equalise the predatory motivation (Cooper, 2000; McKeehan & Sievert, 1996; Shine, 2003), after having spent one week in the laboratory

to habituate them to the food. The test prey were mealworm larvae (*Tenebrio molitor*), which were known to the lizards when tested. Five live prey were placed in the centre of the arena and covered by a transparent plexiglas Petri dish, to prevent the lizard from ingesting the mealworms during the test.

At testing, in both the predatory and exploratory tests, the lizard was gently removed from its cage and placed in a tunnel attached to the entrance of the arena. Thereafter the experimenter, located behind a black cloth blind, lifted up the opaque gateway that prevented the lizard from entering the arena. The test started when the lizard spontaneously left the tunnel and entered the arena. In the predatory tests, the lizard therefore immediately perceived the presence of the prey when leaving the tunnel. The lizard was allowed to move freely within the arena for 5 minutes; during this time, the gateway was not closed, so the lizard could return to the tunnel. At the end of the test, the lizard was returned to its cage and the arena floor was cleaned with ethyl alcohol to prevent any possible effect of chemical cues on subsequent individuals. The tests were carried out at a mean air temperature of $34.6 \pm 0.4^\circ\text{C}$. The test was recorded with a 2.5×3.5 cm colour video camera placed centrally above the arena, and videotaped on a digital support. Videos were later reviewed using the "Virtualdub" video programme, which also permitted frame-by-frame analysis. Lizard behaviour was recorded continuously, using a digital event recorder. We considered the following behaviour parameters and their relative occurrence:

- The first lateral direction of head position in relation to the longitudinal body axis immediately after the lizard emerged from the tunnel.
- The frequency and duration of head position in relation to the longitudinal body axis immediately after the lizard emerged from the tunnel.
- The frequency and duration of body side exposure towards the centre of the arena after fully entering the arena.
- The frequency of the left–right direction of head rotation back towards the prey after departing from them (in predatory tests only).

Statistical analysis was carried out with the SPSS 15.0 for Windows software (SPSS, 2006), using the Wilcoxon Signed-Rank Test (T^+) to compare the durations and the frequencies for both tests. We also used the Chi-Square Component "z" Index (z) (Bishop, Fienberg, & Holland, 1975) to compare the observed frequency of first direction choice against the relative expected frequency. Means are listed $\pm SE$ and the probability, set at $\alpha = .05$, is two-tailed throughout, unless otherwise stated.

RESULTS

When emerging from the tunnel, the lizards stopped at the entrance of the arena and turned their head. More lizards turned their head to the right than to the left in the exploratory tests (36 vs 23, respectively; $z = 1.197$; $p < .05$), but they were equally split between both sides in the predatory tests (22 vs 22). The individual frequency of the subsequent head turns during the exploratory test was 1.41 ± 0.15 to the left and 1.60 ± 0.14 to the right ($T^+ = 1.205$; $N = 68$; $p > .1$), and 1.07 ± 0.19 to the left and 1.13 ± 0.17 to the right in the predatory tests ($T^+ = 0.970$; $N = 68$; $p > .1$). The lizards turned their head, both to the left and to the right, more frequently in exploratory tests than in predatory tests (left: $T^+ = 2.234$; $N = 68$; $p = .03$; right: $T^+ = 2.000$; $N = 68$; $p = .045$). In the exploratory tests, the lizards kept their head turned to the left for an average of 5.4 ± 1.2 s and to the right for 8.9 ± 2.1 s ($T^+ = 2.183$; $N = 68$; $p = .03$). In contrast, during the predatory tests the lizards showed a next-to-significance tendency to keep their head turned longer to the left (5.7 ± 1.4 s) than to the right (3.5 ± 0.8 s; $T^+ = 1.833$; $N = 68$; $p = .068$). They also kept their head turned longer to the right in the exploratory tests than in the predatory tests ($T^+ = 3.254$; $N = 68$; $p = .001$), but they kept their head turned to the left for the same duration in both kinds of test ($T^+ = 0.629$; $N = 68$; $p > .1$). During the exploratory tests, the lizards spent more time with their head turned before entering the arena than during the predatory tests ($T^+ = 2.570$; $N = 136$; $p = .01$).

The lizards entered the arena suddenly with the whole body, and moved freely within it without any apparent fear. During the exploratory tests, they invariably moved near the wall of the arena. In contrast, during the predatory tests the lizards usually approached the prey at the centre of the arena without hesitation when entering the arena. This occurred in 42 (61.8%) tests out of the 68 predatory tests. In the remaining 26 tests (38.2%) they reached the prey under the Petri dish only after moving for a while near the wall of the arena. When entering the arena in the exploratory tests, more lizards initially presented the left body side to the arena centre—i.e., they walked along the side in an anti-clockwise direction—than the right body side (40 times vs 27 times; $z = 1.123$; $p < .05$). In contrast, during the predation tests the first body side presented to the centre—i.e. the prey—was the right side for 31 lizards and the left side for 37 lizards ($z = 0.514$; $p > .05$).

In terms of the total number of body side presentations, we found that lizards in the exploratory tests showed their left side to the centre 3.1 ± 0.2 times per test and their right side 2.6 ± 0.2 times ($T^+ = 2.477$; $N = 68$; $p = .01$). During the predatory tests, they exhibited their left body side to the prey 10.8 ± 0.8 times and their right side 11.3 ± 0.9 times ($T^+ = 0.055$; $N = 68$; $p > .1$). We compared these results in the two kinds of test; the lizards presented both the left and the right side of the body to the centre of the

arena, or to the prey, more frequently in predatory tests than in exploratory tests (left side: $T^+ = 6.893$; $N = 68$; $p < .001$; right side: $T^+ = 6.783$; $N = 68$; $p < .001$). In the exploratory tests the left side presentation lasted 87.1 ± 5.2 s whereas the right side lasted 71.6 ± 6.0 s ($T^+ = 2.009$; $N = 68$; $p = .045$); in predatory tests the lizards presented the left side to the prey for 65.7 ± 5.5 s and the right side for 64.7 ± 5.1 s ($T^+ = 0.055$; $N = 68$; $p > .1$). The lizards kept the left side of the body directed towards the centre of the arena in the exploratory tests longer than to the prey in the predatory tests (87.1 ± 5.2 s vs 65.7 ± 5.5 s; $T^+ = 2.924$; $N = 68$; $p < .01$). In contrast, they directed the right side of the body to the centre of the arena in the exploratory tests and to the prey in the predatory tests for a similar duration (71.6 ± 6.0 s vs 64.8 ± 5.1 s; $T^+ = 0.883$; $N = 68$; $p > .1$).

When withdrawing from the prey in the predatory tests the lizards sometimes stopped and turned their head back towards it. In particular, they turned their head to the right more often than to the left (0.87 ± 0.17 times and 0.59 ± 0.13 times, respectively; $T^+ = 2.138$; $N = 68$; $p = .03$).

Lizards entered the refuge an average of 1.93 ± 0.14 times during the exploration tests and 1.38 ± 0.16 times during the predatory tests ($T^+ = 2.854$; $N = 68$; $p < .01$). The lizards remained inside the refuge for longer during the exploratory tests than during the predatory ones (30.3 ± 2.3 s and 20.1 ± 1.6 s, respectively; $T^+ = 4.405$, $N = 68$, $p < .001$). Finally, each individual stayed inside the refuge for 62.1 ± 5.2 s during the exploratory test and for 34.9 ± 4.6 s during the predatory test ($T^+ = 5.111$; $N = 68$; $p < .0001$).

DISCUSSION

Our results show that the lizards were clearly biased in directing the left eye towards the centre of the arena during an exploratory task. In this kind of test all lizards directed the left side of the body towards the centre of the arena for longer and more frequently, moving very near to the wall. As this wall was opaque, such a behaviour is probably indicative of the use of the left eye for exploration. This is supported by the fact that lizards turned their head significantly longer to the right—i.e., they presented the left side of their head—when exiting the refuge. As the arena was circular, this right turn of the head indicates environmental monitoring with the left eye. This result supports previous findings on the same species, which revealed a preferential left path during exploratory behaviour in a maze and left-eye observation of the environment before entering it (Csermely et al., in press).

During the predatory tests, however, the lizards did not show any preferential directing of either side to the prey, either in frequency or duration. In fact, just as we did not record any preferential right side presentation, we did not find any strong left eye presentation when the arena centre was empty.

In contrast, the predatory test data show a statistical tendency for a longer left head turn (i.e., right eye use) compared to the right one (left eye use), when exiting from the tunnel. This indicates the tendency to use of the right eye to observe the centre of the arena, i.e., the prey. Although the phenomenon was just a tendency, not a true significance, it lies in the opposite direction from the exploratory test, where we found strongly significant use of the left eye. We are confident that the lizards clearly perceived the different contexts in the two tests they experienced, and that their behaviour was thus affected by test type. The reason for such confidence is that during the predatory tests they spent less time turning their head before entering the arena, and also moved without hesitation to the centre to investigate the prey.

Moreover, when the lizards were moving away from the prey and stopped, they frequently turned their head back to it, with a preferential right rotation. This clearly indicates the observation of the prey with the right eye even when it is behind the individual, and thus left hemisphere processing of predatory cues. The highly mobile neck of lizards allows them to perform such behaviour frequently in order to check behind themselves. In fact, both Bonati et al. (2010) and Csermely et al. (in press) reported this behaviour for monitoring a predator or the environment. In particular, those authors observed a left turn bias, unlike during the predatory task in this study. This result thus indicates that the lizards looked at the prey when they turned their head back, and did so preferentially with the right eye.

In the light of these findings, we suggest that the absence of a preferential side presentation towards the prey in the predatory test is due to the likely high level of exploratory motivation that is also observed in some parts of predatory test, which cannot be removed. The presence of exploratory behaviour in a predatory context thus “polluted” the predatory behaviour, preventing it reaching statistical significance. In fact, when predatory behaviour was really separated from exploratory behaviour, as during turning of the head towards the prey at the beginning of the test, and towards the back, this was performed by the right eye, as expected.

We found that prey watching and body presentation to the prey by both sides of the body occurred more frequently in predatory tests than in exploratory ones. This likely demonstrates that during predatory tests the lizards both explore and monitor the prey. Several previous studies have demonstrated how lateralised animals perform more tasks at the same time more efficiently than non-lateralised ones (Dadda & Bisazza, 2006b; Fabre-Thorpe, Fagot, Lorincz, Levesque, & Vaclair, 1993; Güntürkün et al., 2000; Rogers et al., 2004). When comparing lateralised and non-lateralised chicks, Rogers et al. (2004) showed how individuals with a specialised bias to look at grains on the floor preferentially with the right eye, while monitoring a simulated raptor with the left eye, pecked more grains than non-specialised chicks. Hence, individual advantage is

independent of the direction of lateralisation (with only one alternative), but is related to the opposite brain processing of dual tasks (Vallortigara et al., 1999), as in our lizards. Nevertheless, the presence in the population of the same preference for the same kind of stimuli could be the result of an evolutionarily stable strategy, whereby asymmetric lizards must coordinate their behaviour with that of other asymmetric organisms with which the lizards interact, for example raptor birds (Ghirlanda & Vallortigara, 2004).

In conclusion, our findings show a strong left eye/right hemisphere preference during exploration of the environment, which, however, is not readily detected in the presence of prey. Our results also show the tendency to observe the prey with the right eye, in accord with previous observations in the same and different species (Bonati et al., 2008; Csermely et al., 2010; Lippolis, Joss, & Rogers, 2009; Vallortigara & Rogers, 2005). Moreover, since our tests were carried out in the same individuals, we confirm that visual lateralisation in lizards allows the simultaneous performance of important day-to-day behavioural tasks, such as feeding and exploratory vigilance, and also probably antipredatory vigilance.

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