Laterality: Asymmetries of Body, Brain and Cognition

Lateralisation in a detour test in the common wall lizard (Podarcis muralis)

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Detour tests provide a reliable indicator of the presence of visual lateralisation. Previous studies on fishes and birds suggest that preferences in choosing to detour an obstacle to reach a goal are due to asymmetries of eye use. We studied detour behaviour to reach a prey in males of *Podarcis muralis* in order to ascertain visual laterality for a predatory task. Lizards were found to be lateralised at both individual and population levels, although only a few lizards were found to express lateralisation at the level of the individual. The preferential direction of detouring is the left route around a transparent barrier, indicating a right eye/left hemisphere use to observe the prey and confirming the results of recent work. The eye used to fixate the prey was maintained longer in the same direction the lizards subsequently chose to approach it, confirming that the preference was basically due to visual asymmetry, not to motor asymmetry. To our knowledge this is the first study of detouring conducted on sauria, demonstrating how these lizards are right eye/left hemisphere lateralised for predatory tasks at individual and population level.

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

Evidence of existence of cerebral lateralisation, the hemispherical specialisation of specific functions manifested as the asymmetrical use of the two sides of the body, have been found in the last three decades among many mammals and birds, and more recently also in ectotherms (Vallortigara & Bisazza, 2002).

The disparate findings of anatomical, and then behavioural, asymmetries in those animals suggest that the lateralisation is likely not the result of evolutionary convergence, but a plesiomorphic character, inherited from a common ancestor (Andrew, 2002). The lateral eye position of many vertebrate species, such as most ectotherms and birds, allows them to respond differently to some kinds of stimuli viewed either from the left- or right-hand side. Differences in processing strategies carried out by either hemisphere may lead to a preference for choosing to monitor a given stimulus with the left or the right eye, indicating that the contralateral hemisphere is specialised for controlling the corresponding response (Andrew, 1983; Andrew & Dharmaretnam, 1993; Rogers, Zappia, & Bullock, 1985). Visual asymmetry, indeed, seems widespread among animal species with lateral eyes (Rogers & Andrew, 2002; Vallortigara, Rogers, & Bisazza, 1999b).

Detour tests are an interesting method to evaluate visual asymmetry, originally used with birds (Regolin, Vallortigara, & Zanforlin, 1994, 1995; Vallortigara, Regolin, & Pagni, 1999a), and then in fishes (Facchin, Bisazza, & Vallortigara, 1999; Bisazza, Pignatti, & Vallortigara, 1997a, 1997b; Bisazza, Facchin, Pignatti, & Vallortigara, 1998). Leftward or rightward bias in reaching a goal behind an obstacle is considered to be due to asymmetries of visual, rather than motor, processing (Bisazza et al., 1997a; Facchin et al., 1999), and thought to be associated with the need for individuals to maintain visual fixation and analysis of a goal object within a monocular lateral field (Zucca & Sovrano, 2008; Vallortigara et al., 1999a, 1999b). Monocular eye use for observing environmental cues provides analytical processing of a stimulus different from that generated by binocular viewing, and avoids the possibility of computational competition occurring between the brain hemispheres when responding to the stimulus ("functional incompatibility": Sherry & Schachter, 1987). However, monocular viewing is likely preceded by an initial period of binocular viewing, followed by the decision to use one eye only for monocular viewing.

The lateralisation of function might also be advantageous to an individual because it may favour simultaneous and parallel processing of information in both monocular fields. Lateralised vertebrates appear to possess the ability to process complementary and contrasting information simultaneously and efficiently, without constraining the performance of alternative and concurrent cognitive tasks, such as vigilance and other important activities, including feeding (Rogers, 2000; Rogers, Zucca, & Vallortigara, 2004). Lateralised domestic chicks (*Gallus g. domesticus*) perform better both food pecking and vigilance in presence of an aerial predator model than non-lateralised chicks, which instead show interference between those tasks and limitation in their performance (Rogers et al., 2004).

The direction of visual asymmetries, in fact, is task and stimulus dependent, connected to some daily activities including social interactions (Dadda, Sovrano, & Bisazza, 2003; Hews, Castellano, & Hara, 2004), foraging (Rogers, 2000), and vigilance behaviours (Brown, Western, & Braithwaite, 2007; Robins & Rogers, 2004). Toads (genus *Bufo*) have a right-predatory and a left-agonistic visual hemifield control for tongue strikes (Vallortigara, Rogers, Bisazza, Lippolis, & Robins, 1998), and the green tree frog (*Litoria caerulea*) has a significantly left-eye preference when directing agonistic responses (Robins & Rogers, 2006b). Prey discrimination and catching, in particular, seem controlled by the right eye/left hemisphere, which is commonly involved in motivated decisions (Robins & Rogers, 2006a; Vallortigara & Rogers, 2005), as widely documented in a variety of birds, such as chicks (Andrew, Mench, & Rainey, 1982; Rogers, 1997), zebra finches (Alonso, 1998), pigeons (Güntürkün, 1985), tits and corvids (Clayton & Krebs, 1994), quails (Valenti, Sovrano, Zucca, & Vallortigara, 2003), and black-winged stilts (Ventolini et al., 2005).

Lizards are highly interesting subjects for laterality studies because of the lateral position of their eyes, which minimises the range of the binocular field, and, in a feature common to ectotherms, the absence of a large corpus callosum (Deckel, 1995) that would otherwise facilitate communication between the two hemispheres. The visual system of *Anolis* lizards permits a hemisphere to be ''unaware'' of what the other perceives (a sort of ''split brain'': Deckel, 1995). Considering the predatory behaviour in sauria, there is just one report devoted to lateralisation: it concerns the agamid *Ctenophorus ornatus* which prefers to control predatory responses with the right eye (left hemisphere) and this preference seems to become stronger with familiarisation with the prey. The direction of visual lateralisation could change with habituation to the prey, affecting the codification of predatory cues (Robins, Chen, Beazley, & Dunlop, 2005). Experience then may affect direction bias. Consequently, experience may help the reptile brain to elaborate different incoming visual information perceived from the environment (Robins et al., 2005).

In this study we aimed to observe laterality in the lacertid common wall lizard (*Podarcis muralis*) in a predatory context, using a detour test to reach a known prey. Knowing that the right eye (left hemisphere) is usually involved in controlling stimuli generated by potential prey, we hypothesised that lizards would prefer to monitor prey within the right visual field while detouring a transparent obstacle. Consequently we expected to record significantly more left-routes (right-eye use preferring) than right-routes (left-eye use preferring) to be taken by lizards to detour the obstacle during testing.

METHOD AND MATERIALS

We collected 16 adult male *Podarcis muralis* lizards from scattered small populations in Parma, captured by noose, a harmless and widespread catching method. They were put in cloth bags immediately after and carried to the laboratory, where they were housed in $120 \times 50 \times 50$ cm wood terraria. These had the front and one lateral side in glass, a 2×2 mm wire mesh ceiling, the floor covered with sand, and one pebble and one brick for refuge and/or basking site; water was provided *ad libitum*. The terraria were located in a former greenhouse, with full glass sides, but an opaque roof; light, photoperiod and temperature were therefore natural, although artificial light and heat could be provided if necessary.

Once in 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- to 3-day intervals, to acclimatise to the new environment and diet. After the first week the individuals were food deprived for 3 days before the tests (cf. Cooper, 2000; McKeehan & Sievert, 1996; Shine, 2003) to induce and equalise the predatory motivation. The test sequence protocol lasted approximately 15 days, and the lizards therefore remained in captivity for no more than 3 weeks. At the end of the experimental period they were released at the same site of capture. None of the lizards was harmed by the experiment, which was carried out under licence from Italian authorities.

The experimental apparatus consisted of one PVC T-maze (Figure 1), covered with transparent and colourless Plexiglas strips. The central arm of the maze ($8 \times 30 \times 6$ cm) had a rear entrance for the lizard, while the opposite end was the entrance to the cross arm ($8 \times 15 \times 6$ cm), which was prevented by a sliding sluice gate, remotely operated by the observer via a cable. At the centre of the maze cross arm there was a 4×8.5 cm Plexiglas barrier (Figure 1) with a 1×1 cm wire mesh attached to its rear side, to ensure the lizards perceived the barrier presence but did not have the opportunity to climb it. Behind the barrier the lizard could see a prey, but had to detour the barrier to reach it. The access to this arm of the maze was limited to a passage 4 cm wide, to induce the lizard to have the head aligned with the body axis when entering the cross arm and then having a standardised central position with respect to the prey. This was also to ensure that the lizards had an unbiased view of the prey on the visual midline, before choosing either detour direction.

We used one mealworm larva (*Tenebrio molitor*) as prey, then already known to the lizards at testing. We froze the larva to avoid the possibility that its different movements could affect the lizard's choice in the tests. A colourless, transparent glass Petri dish (4 cm in diameter, 2 cm high)
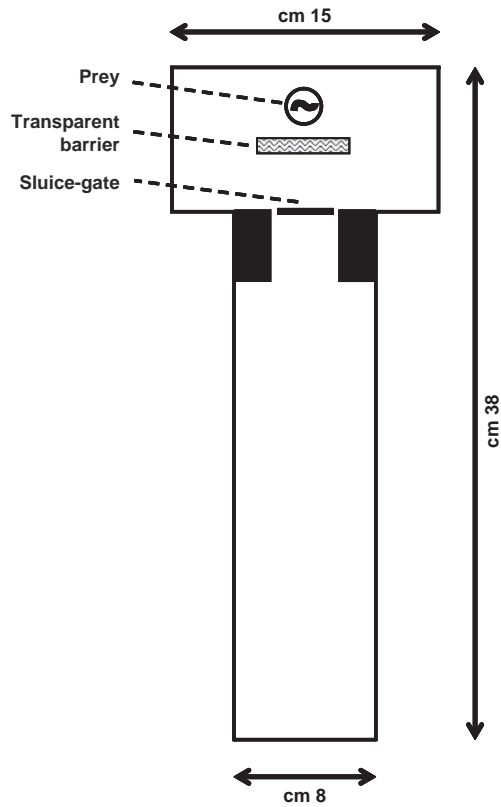
Figure 1.   A sketch of the experimental apparatus.

covered the prey, preventing the lizard from ingesting the mealworm at the end of the test.

At testing, each individual was gently induced to enter the central arm of the maze, which was then closed. Here they remained for 15 minutes to acclimatise. The test started when the sluice gate was lifted up and ended when the lizard reached the prey, whereas it was considered void if the lizard refused to approach the prey within 20 minutes. The test was recorded with a 2.5×3.5 cm black and white video camera placed centrally in front of the maze and videotaped on a digital support. The videos were later reviewed using the "Virtualdub" video software, 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: latency in the first movement, latency in entering the cross arm, latency in the first attempt to prey, detour direction chosen to reach the prey, frequency and duration of head position in relation to the

longitudinal body axis with respect to the target prey: right-hand side head positioning, left-hand side head positioning, central head positioning, and frequency of tongue flicking.

Our aim was to repeat the tests 10 times maximum for each individual, with a minimum interval of 60 minutes between tests to limit the danger of pseudoreplication; however that was not achieved in every lizard. In some cases, in fact, they ignored the target prey and demonstrated exploratory behaviour of the maze; we did not consider these data. We judged "exploratory" tests as those in which the lizard detoured the barrier and bypassed (or trod on) the prey, or when the lizard did not detour but tried to escape through the lateral arms of the maze. We considered a "predatory" test only when the lizard, after detouring the barrier, attempted to eat the prey under the Petri dish. Each lizard was tested three times daily maximum and tested again after 3 days. During the last (third) daily test we removed the glass Petri dish that covered the prey, allowing the lizard to eat it, to reduce habituation or extinction of response to the prey. The maze floor was cleaned with ethylic alcohol before the beginning of every test to remove chemical cues that could possibly influence the subsequent choice.

Maze floor temperature was measured with a $5 \times 2.2 \times 1$ cm temperature data-logger fixed to the experimental apparatus, downloading the data with MTT Tempstick software. The floor temperature during the tests was maintained at a consistent 30.9 ± 0.2 °C.

We used the Kruskal-Wallis ANOVA (KW) to compare behaviour durations and tongue-flicking frequency, and the Mann-Whitney-Wilcoxon test (W_x) to compare both head rotation duration and observation durations with different eyes. The cumulative frequency of either detour direction against the relative expected frequency were compared with both the parametric One sample t-test (t) and the Nonparametric Mann-Whitney-Wilcoxon test (W_x) test. All these tests were calculated with the SPSS 14.0 for Windows software (SPSS, 2006). We also used the Binomial test to ascertain the lateralisation at the individual level (Siegel & Castellan, 1988). Means are listed $\pm SE$ throughout and the probability, set at $\alpha = .05$, is two-tailed throughout, unless otherwise stated. When comparing the detouring directions we used both two-tailed and one-tailed statistical analyses. On the basis of a recent work (Bonati, Csermely, & Romani, 2008) we considered the one-tailed statistics expecting a preference for the left detouring route.

RESULTS

While detouring the barrier to reach the prey, the lizard could monitor it with a monocular visual field and we considered such a bias as indication of initial choice. We recorded the lizards, after they reached the cross arm,

keeping the head along the body axis 89 times total (binocular vision), in contrast to turning the head to the left-hand side (right eye use) 218 times in total, and to the right-hand side (left eye use) 191 times in total. The lizards remained at that location for 2.2 ± 0.4 seconds, keeping the head aligned to the body axis, but for 6.0 ± 1.2 seconds turning the head to the left-hand side and 4.5 ± 0.7 seconds to the right-hand side ($KW = 56.560$, $N = 3$, $p < .01$). The individuals kept the head turned to the left-hand side or to the right-hand side for variable durations ($KW = 39.921$, $N = 16$, $p < .001$ and $KW = 34.618$, $N = 16$, $p < .01$, respectively). In particular, the lizards spent more time watching the prey with the right eye than with the left eye overall ($W_x = 2.814$, $N = 191$, $p < .01$).

Moreover, when the lizards decided to reach the prey with a left path, the total time spent in each test using the right eye to watch the prey was longer than when using the left eye ($W_x = 4.502$, $N = 48$, $p < .001$) (Figure 2). Conversely when lizards attempted to catch the prey with a right path, the total time spent in each test using the left eye was longer than when using the right eye ($W_x = 7.633$, $N = 81$, $p < .001$).

Over the experimental period the lizards returned at least six tests each that included valid predatory responses which were not otherwise discarded due to inattendance to the prey (Table 1).

Only five (31.3%) individuals were lateralised, showing a preference for the same direction in most of their tests 7 from 8, 6 from 6, 9 from 10, 6 from
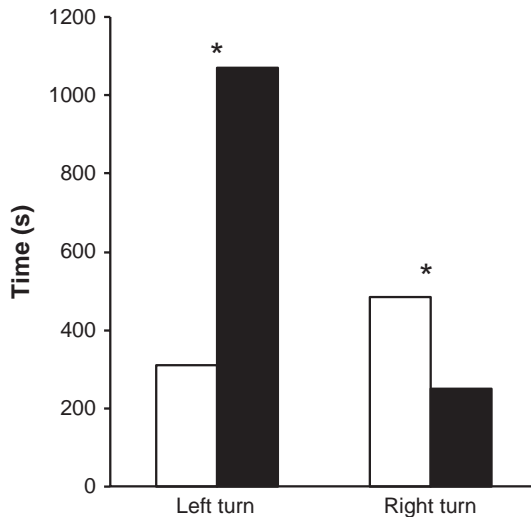
Figure 2. The total time spent by the lizards using either eye to watch the prey in each test, when they routed to the left or to the right to reach the prey. White columns: left eye; black columns: right eye. $*p < .001$.

TABLE 1
Tests and routes

Lizard	Left route	Right route	One-tailed p
1	9	1	.005
2	6	0	.008
3	7	1	.016
4	6	1	.028
5	5	2	.082
6	5	2	.082
7	6	4	.103
8	6	4	.103
9	6	4	.103
10	5	3	.110
11	5	4	.123
12	5	5	.123
13	3	4	.137
14	3	5	.110
15	2	4	.117
16	2	8	.022
Total	81	52	

The number of tests when the lizards approached the prey to detour behind the barrier and the one-tailed probability obtained by binomial test for every individual. The lizards are ordered in descending significance and left-route preference for detouring.

7, 8 from 10, respectively; Binomial test (two-tailed): $p < .05$, $p < .05$, $p < .01$, $p = .055$, $p < .05$, respectively (see Table 1). On the other hand, assuming that the lizards preferred to detour the barrier using a specific route, which allowed them to check the prey with the right eye while detouring, we considered the same results with the one-tailed p too: $p < .025$, $p < .025$, $p < .005$, $p < .03$, $p < .025$, respectively) (see Table 1). Analysing the population as a whole, the lizards chose to detour the barrier 81 times (60.9%) at the left hand side from 133 total and 52 times at the right hand side $t = 2.046$, $N = 16$, p (two-tailed) $= .059$; $W_x = 1.979$, $N = 16$, p (two-tailed) $= .048$. Again, assuming that the lizards preferred to detour the barrier using a specific route, we considered the same results with the one-tailed p too: $t = 2.046$, $N = 16$, $p = .029$; $W_x = 1.979$, $N = 16$, $p = .024$. If we consider the direction chosen by the five lateralised lizards only, we find a preference for the same (left) direction for four lizards from five.

DISCUSSION

Our results show that some lizards are lateralised at the level of the individual, having a preference to maintain familiar prey within the right monocular field by consistently detouring with a left path around an

obstacle to reach the prey. The data also reveal a significant right eye/left hemisphere preference to observe the prey from distance, although the percentage of such individuals is moderate. Nevertheless this bias is confirmed by the preference in the population to use the right eye to look at the prey for more time.

Moreover, the forms of individual- and population-level lateralisation reported here i.e., detour preferences and the preference to maintain a specific head posture with respect to prey viewed from a distance are entirely in accord with similar types of predatory responses found to be lateralised in other vertebrates. In fact, preferences in detour behaviour probably do not arise from motor lateralisation phenomena, but from asymmetry of eye use (Bisazza et al., 1997a; Facchin et al., 1999; Vallortigara et al., 1999a, 1999b), found to be widespread in animals with laterally placed eyes (Vallortigara et al., 1998), including lizards. In sauria, moreover, most of the optic nerve fibres decussate completely and a limited commissural system connects the hemispheres (Butler & Northcutt, 1971). This could make the two halves of the brain able to work almost independently (Deckel, 1995), each one controlling different functions. Nevertheless, the presence of a little intercommunication between the two halves of the brain does not constrain these animals watching with a specific eye only.

Furthermore, we found a strong relation between the total duration of viewing preference for the prey in each test and the subsequent direction chosen to approach it: eye use was maintained longer in the direction in which the lizards subsequently chose to detour (Figure 2). This shows that they prefer to observe the prey with a specific eye and consequently move in the same direction where that eye is fixated. This is further confirmation of how a visual asymmetry may influence subsequent preferences in motor behaviour, supporting recent hypotheses regarding the contributing to ascertain the perceptual or motor origin of lateralisation (Vallortigara et al., 1999; cf. also Andrew, Tommasi, & Ford, 2000).

The direction chosen in detouring the barrier to reach the prey was the left route for the majority of individuals, indicating a right eye (left hemisphere) use bias for the predation task. In accord with this, the time the lizards spent watching the prey with the left eye was longer than with the right eye, confirming the preferential use of the left eye/right hemisphere for predatory cues. The number of choices for the left path in detouring is indicative of lateralisation at population level, although the low number of individuals shown to be lateralised does not allow a strong conclusion. Moreover, no significant influence of repetition in sequential tests was found, confirming independence and randomness in the performance of the lizards.

As a whole, our results reveal that common wall lizard males are lateralised, because they fixate the prey with a preferential eye (and process

the relative information predominately with the contralateral hemisphere). Furthermore, the direction of such a lateralisation (the right eye/left hemisphere) is consistent across the population. This is in accord with a previous study conducted in the predatory context in the same species (Bonati et al., 2008), as well as with studies of other vertebrates (Robins, 2005; Robins & Rogers, 2004; Vallortigara & Rogers, 2005; Vallortigara et al., 1998). This is a confirmation that the vertebrate brain left hemisphere (therefore input received by the right eye) apparently controls detailed processing of prey stimuli, being associated with the relative decisions, and that the predatory behaviour itself is then lateralised.

Knowledge about predatory behaviour lateralisation in the sauria is poor. There is only one report about the agamid lizard *Ctenophorus ornatus*, which is specialised to observe prey with the right visual hemifield, indicating a left hemisphere specialisation to control predatory functions (Robins et al., 2005). Moreover, in *C. ornatus* the preference increases with familiarisation with the prey, as recorded in toads too by Robins and Rogers (2006a). This is indicative of a different control of novel and familiar prey visual cues by the two halves of the brain, being revealed by different direction of lateralisation. This could reveal a relation between direction bias and experience or long-term memory, which may cause a switch of hemifields responding to the same kind of cues (Robins and Rogers, 2006a).

Experience could then determine a different brain processing. Females of wild *Brachyraphis episcope* (Poeciliidae) from high and low predation pressure areas showed a different response in a detour test. There was a strong lateralisation in 45% of the population exposed to high predatory pressure, against just 15% of others (Brown et al., 2007). If we consider that in our experiment we collected lizards from areas likely suffering different predation pressure, this may explain the low percentage of lateralisation we found and the high variability in their behaviour. Lateralisation may have evolved as an adaptive character responding to environmental need to daily execute several vital tasks, such as monitoring and feeding, at the same time in high predation pressure areas (Rogers et al., 2004).

In other cases the direction of laterality could switch from side to side, as in altering the fear during the test execution or manipulating sexual motivation (Bisazza et al., 1997b, 1998; Brown et al., 2007). Vallortigara et al. (1999b) state that the direction of lateralisation is not very important, considering that there are only two possibilities of outcome, but rather the different direction for different tasks is important. This is because one further advantage of presenting lateralised responses may be the possibility of performing more vital tasks simultaneously without constraining the processing of either of them (Rogers, 2000; Rogers et al., 2004).

In conclusion, our study demonstrates how males of *Podarcis muralis* are lateralised at an individual level. The direction of lateralisation for detour

behaviour in a predatory context is left, indicating a right eye/left hemisphere control at the population level, and confirming previous reports in similar contexts. Moreover, to our knowledge this is the first evidence of a detour lateralisation in sauria and of visual lateralisation in a lacertid lizard, confirming that lateralisation is a widespread phenomenon among the ectotherms. It also supports the hypothesis that vertebrate lateralisation is inherited from a common ancestor and was preserved during evolution as an advantageous character.

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