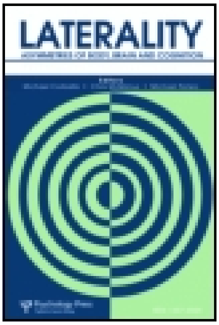

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Looking at a predator with the left or right eye: Asymmetry of response in lizards

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Looking at a predator with the left or right eye: Asymmetry of response in lizards

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Studies carried out with the common wall lizard (*Podarcis muralis*) revealed preferential use of the left eye during responses to predatory threat in laboratory settings and in the wild. Here we tested lizards under monocular conditions of vision, using temporary eye-patching. Lizards were facing a (simulated) predatory threat laterally, from the side of the non-patched eye. Results showed that lizards with the left eye uncovered during predatory threat used the left eye to monitor the predator, whereas lizards with the right eye uncovered nonetheless tried to use the covered left eye. Moreover, lizards frequently tried to change the eye exposition, making a body C-bend behaviour. Right-eyed lizards showed more frequent and faster C-bending responses than left-eyed lizards, trying to monitor the predator with the left eye even though it was patched. Results fit with asymmetries in spontaneous eye use observed in laboratory conditions and in the wild in this species, confirming that structures located on the right side of the brain (mainly served by the left eye) predominantly attend to predatory threat.

Keywords: Common wall lizard; Escape behaviour; Monocular vision; *Podarcis muralis*; Visual lateralisation.

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We know that brain and behavioural lateralisation is widespread in animals, both vertebrates (MacNeilage, Rogers, & Vallortigara, 2009; Rogers & Andrew, 2002; Vallortigara, 2000; Vallortigara, Chiandetti, & Sovrano, 2011) and invertebrates (Ades & Ramires, 2002; Anfora et al., 2011; Hobert, Johnston, & Chang, 2002; Rogers & Vallortigara, 2008). Some recent studies have revealed behavioural lateralisation in the common wall lizard (*Podarcis muralis*) for predatory, exploratory, and antipredatory behaviour (Bonati, Csermely, & Romani, 2008; Csermely, Bonati, López, & Martín, 2011). Bonati, Csermely, López, and Martín (2010) found a bias to left eye use in escape behaviour induced by a simulated predator attack. A left eye dominance in eliciting escape response has been demonstrated in several vertebrate taxa such as fishes, toads, and birds (Vallortigara & Rogers, 2005; Vallortigara, Rogers, & Bisazza, 1999) and many studies (Dill, 1977; Koboroff, Kaplan, & Rogers, 2008; Lippolis, Bisazza, Rogers, & Vallortigara, 2002) have suggested that lateralisation of antipredatory behaviour is associated with a left eye/right hemisphere dominance pattern among vertebrates (note that in animals with laterally placed eyes information entering each eye is mostly processed by contralateral structures in the brain; Vallortigara et al., 1999). Laboratory studies in lizards also agree with evidence obtained under natural conditions: Martín, López, Bonati, and Csermely (2010) found that common wall lizards tested in the wild looked at a predator preferentially with the left eye.

However, the evidence collected so far in lizards concerns biases in spontaneous eye use or turning behaviour. Monocular tests have largely been used in order to study visual lateralisation in vertebrates. This kind of test is of course crucial for revealing asymmetry of function in animals with laterally placed eyes that have a complete decussation of the optic nerve fibres, such as lizards. In fact a forced monocular stimulation could allow us to be sure that the behavioural response is likely controlled by contralateral hemisphere and is actually elicited only by the stimulus we present (Vallortigara et al., 2011). To the best of our knowledge the present study is the first attempt to investigate lateralisation of lizards' antipredatory behaviour employing a monocular occlusion technique. On the basis of the evidence obtained under spontaneous eye use, we expected that lizards would respond more efficiently to predatory threats when using their left eye.

METHOD AND MATERIALS

Housing

From April to September 2011 we collected by noosing 46 adult common wall lizards (*Podarcis muralis*), 26 females and 20 males, from scattered populations within Northern Italy. Lizards were then maintained in

49 × 29 × 25 PVC cages with sand substratum and one rock for hiding and basking. They were fed daily mealworm larvae (*Tenebrio molitor*) and water was provided *ad libitum*. Photoperiod and temperature were natural. Lizards stayed in captivity for 1 day for acclimatising to laboratory conditions before starting the experiments. At the end of the experimental period they were released at the same site of capture. None of the lizards was harmed during the tests.

Eye-patching

The eye-patch consisted of a piece of opaque cotton cloth cut specifically for each lizard to fit the area around the eye we wanted to cover. The eye-patch was fixed by Bostik® glue, a glue totally harmless to horny and frequently renewed lizard skin, which was spread with the help of a wooden toothpick on the area immediately around the eye. A total of 23 animals were patched on the left eye (9 males and 14 females), and 23 were patched on the right eye (11 males and 12 females).

After positioning the eye-patch each lizard was individually stimulated by simulating an attempt to grab it from the side with the covered eye, to test the effectiveness of the patch, and similarly from the side with the uncovered eye. Then eye-patched lizards were maintained singly for 24 hours in an empty cage to prevent the removal of the patch and for them to become accustomed to the eye-patch. No lizards removed the patch before the test. Immediately after that they were tested. At the end of the test, individuals returned to their home-cages. All lizards spontaneously removed the eye-patch within a few hours after the end of the experiment (we did not remove the eye-patch in order to avoid all unnecessary potentially stressful manipulations).

All lizards that participated in the present experiment were naïve as to the test procedure and captivity. Each lizard was eye-patched and tested only once.

Testing

The lizards were introduced into the experimental apparatus which consisted of a 50-cm diameter and 14-cm high circular PVC arena. The wall of the arena was covered with opaque black paint. This prevented the subjects from seeing the external environment. The experimental apparatus was homogeneously lit by natural illumination. At test, each individual was gently induced to enter a 19.8-cm long transparent PVC tunnel (width 5.0-cm) in the middle of the arena (Figure 1a). This was done in order to guarantee that at the beginning of the test the animal was in the appropriate starting position (at the centre of the arena) with its body aligned on its longitudinal axis.

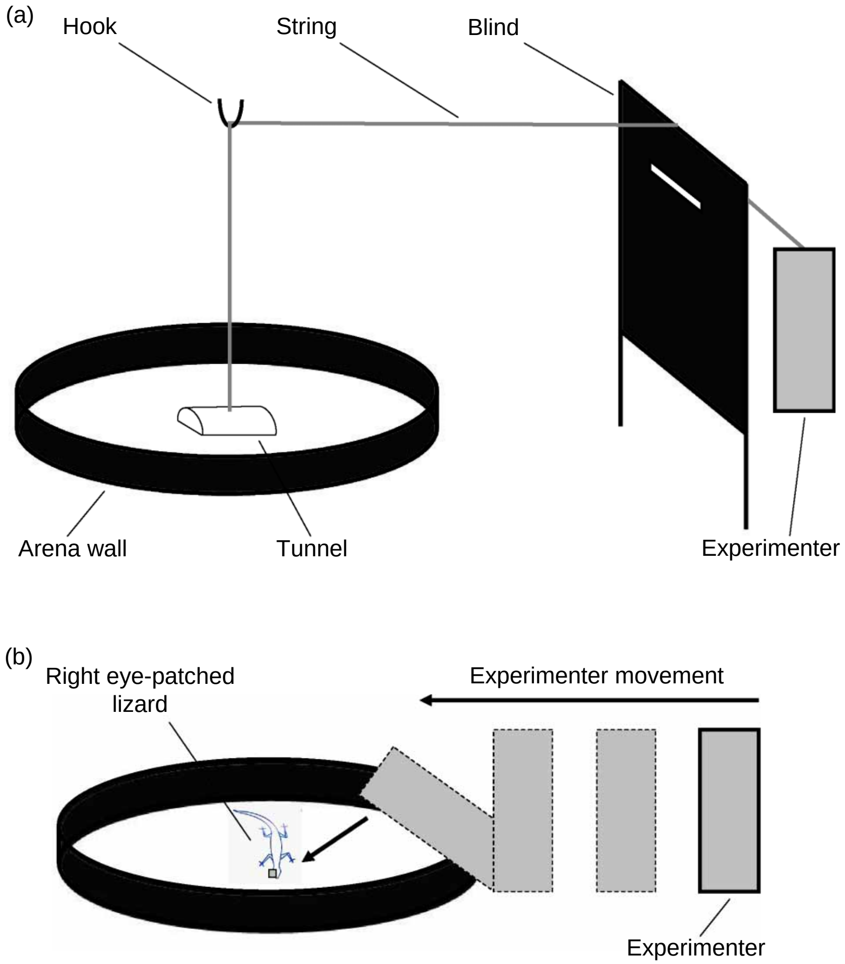

Figure 1. (a) The experimental apparatus at the beginning of the test. Lizards are inside the tunnel. (b) A representation of a right eye-patched lizard, stimulated from the left eye side. Once positioned very close to the arena wall the experimenter approached the lizards from above with "claw hands".

The tunnel was then lifted using a string controlled by an experimenter who was positioned away from the arena, then the experimenter simulated a lateral predator approach from above by walking towards the lizard and attempting to capture it with "claw-hands" (Figure 1b). This stimulation was devised to reproduce a bird attack and was done by the same experimenter throughout the study. The stimulation presentation was lateral and took place for each animal from the non-patched eye side (Figure 1b). Each lizard was stimulated by the predatory attack three times overall, in a way that depended on its positioning with respect to the experimenter following the previous attack. For instance, if after being stimulated the first time a lizard escaped and it positioned itself facing the experimenter with the patched eye, the test was interrupted and the lizard returned in its home-cage. On the other hand, if the lizard faced the experimenter with the unpatched eye it was stimulated again. The experimenter moved to a position in order to approach the lizard laterally as for previous stimulations. A line on the floor around the arena indicated the starting point for the attack. As after first stimulation lizards changed their position and distance from the wall of the arena, we analysed second and third stimulation latencies separately.

All tests were recorded with a digital mini DV colour video-camera 17.0 × 9.0 × 8.0 cm placed above the arena in order to record movements in any direction. The camera was positioned on a tripod at a height of 180.0 cm from the arena surface. The test was subsequently analysed using the file obtained from the video-camera. Frame by frame analysis was made possible by using Virtualdub video software. The lizard behaviour was recorded continuously, using a digital event recorder, and we measured the following behaviours:

- Flight latency (time in seconds from the beginning of the stimulation and the beginning of the flight). It was named first, second, or third depending on the stimulation that elicited it.
- Frequency of body C-bend behaviour after the stimulation (number of times that lizards bent their body to move in the opposite direction).
- Direction of body C-bending (clockwise or anticlockwise).
- Duration of body C-bending for either direction (time in seconds from the beginning of the turn to the new alignment of the body; tail alignment was not considered).
- Eye exposed towards the predator during the first, second, and third flight.
- Eye exposed towards the predator when the lizard stopped the flight.

Statistical analyses

Data were analysed with the PASW Statistic 18.0 for Windows software (SPSS, 2011). We used the Kolmogorov-Smirnov test (*D*) to evaluate flight latency distribution. A factorial ANOVA was used on reciprocal transformed data to analyse the flight latencies for both left and right monocular stimulations. Binomial tests were used to compare frequencies of C-bending, and frequencies of eye exposed towards the predator during and after the flights. As second and third stimulations depended on previous stimulations (pseudo-replications), first, second, and third latencies and eye exposition towards the predator were compared independently. We used the Mann-Whitney test (*U*) to compare left and right flight latencies and C-bend durations for clockwise and anticlockwise rotations. Means are shown with ± *SE* throughout and the probability, sets at $\alpha = .05$, was two-tailed throughout.

RESULTS

After removing the tunnel the lizards remained motionless. When the experimenter moved towards them the lizards escaped towards the black wall of the arena. Left eye-patched lizards moved with a first flight latency of 2.39 ± 1.04 seconds, and right eye-patched lizards with a first flight latency of 2.27 ± 0.86 ($U = 0.440$, $N = 46$, $p = .660$). Once stopped close to the arena wall, 39 lizards (21 left eye-patched and 18 right eye-patched) exposed the unpatched eye to the centre of the arena and were stimulated again. Following the second stimulation left eye-patched individuals showed a flight with a latency of 1.17 ± 0.41 seconds, whereas right eye-patched individuals showed a latency of 0.58 ± 0.09 s ($U = 0.155$, $N = 39$, $p = .876$). Then 29 lizards (14 left eye-patched vs 15 right eye-patched) were stimulated again. Left eye-patched lizards escaped with a latency of 0.86 ± 0.28 s whereas right eye-patched lizards escaped with a latency of 0.59 ± 0.12 s ($U = 1.296$, $N = 27$, $p = .200$). No difference in left vs right eye-patched individuals' latency to flight was apparent (transformed 1/ × data, $F = 0.586$, $p = .446$). A similar trend of first, second, and third mean latency was observed between left and right eye-patched individuals

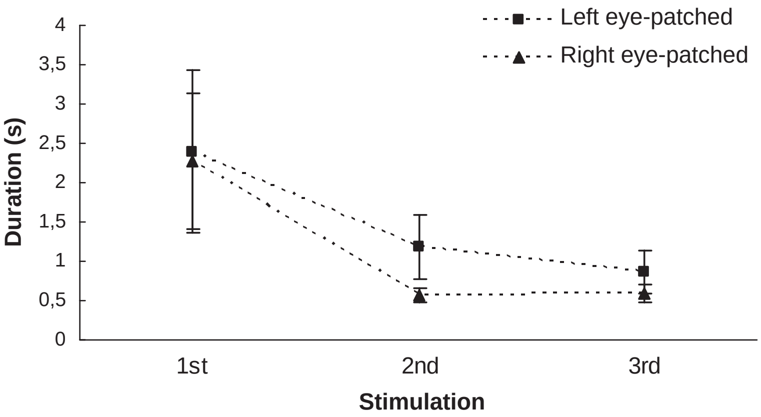

Figure 2. Mean flight latency after first, second, and third stimulation in left and right eye-patched lizards. Latencies have a similar trend (transformed 1/ × data, $F = 2.900$, $P = .059$). Right eye-patched lizards (i.e., lizards that used the left eye in order to monitor) showed shorter latencies but the effect was not statistically significant.

(transformed 1/ × data, $F = 2.900$, $p = .059$; Figure 2). We compared left and right eye-patched flight latency between and within sexes; then we compared latencies between sexes within left and right eye-patched groups. No difference was apparent.

When stimulated by predatory threat all lizards escaped. Among left eye-patched lizards, 10 out of 19 lizards exposed towards the predator the uncovered (right) eye (Binomial test, $p = .176$); 4 lizards ran away exposing the back of the body (Table 1). Among right eye-patched lizards, 16 out of 20 exposed the uncovered (left) eye (Binomial test, $p = .005$); 3 lizards exposed the back (Table 1). After the first run, lizards stopped against the black wall of the arena and monitored the experimenter. During these stops 10 left eye-patched individuals exposed the uncovered right eye towards the predator and 13 exposed the covered eye (Table 2; Binomial test, $p = .136$). In contrast, when the patched eye was the right eye, 16 out of 23 lizards exposed the uncovered left eye (Table 2; Binomial test, $p = .029$). Analysing the escape behaviour of lizards that were subjected to the second stimulation, we observed that when they had their left eye patched they exposed the uncovered right eye during the run 13 vs 6 times (Binomial test, $p = .05$; Table 1); 2 lizards exposed the back. When they had their right eye patched, on the other hand, lizards exposed the uncovered left eye 14 vs 4 time during the run (Binomial test, $p = .012$; Table 1); no lizards exposed the back. We

TABLE 1
Eye exposed towards predator during flight after first, second, and third stimulation in both left and right eye-patched lizards.

	Left eye patched				*Right eye patched*			
Eye exposed	*Left*	*Right*	*Back*	*Total*	*Left*	*Right*	*Back*	*Total*
First stimulation								
Females	7	5	2	14	9	2	1	12
Males	2	5	2	9	7	2	2	11
Total	9	10	4	23	***16	***4	3	23
Second stimulation								
Females	2	9	2	13	9	1	0	10
Males	4	4	0	8	5	3	0	8
Total	*6	*13	2	21	**14	**4	0	18
Third stimulation								
Females	3	5	1	9	9	0	0	9
Males	2	3	0	5	6	0	0	6
Total	5	8	1	14	***15	***0	0	15

Statistical results refers to left vs right eye exposition. * = .07 < p < .05, ** = .05 < p < .01, *** = p < .01.

TABLE 2
Eye exposed towards predator during stops (immediately after flight) after first, second, and third stimulation in both left and right eye-patched lizards

	Left eye patched				*Right eye patched*			
Eye exposed	*Left*	*Right*	*n/a*	*Total*	*Left*	*Right*	*n/a*	*Total*
First stimulation								
Females	8	6	0	14	10	2	0	12
Males	5	4	0	9	6	5	0	11
Total	13	10	0	23	**16	**7	0	23
Second stimulation								
Females	3	9	1	13	9	1	0	10
Males	3	4	1	8	5	3	0	8
Total	*6	*13	2	21	**14	**4	0	18
Third stimulation								
Females	3	5	0	8	9	0	0	9
Males	2	3	1	6	6	0	0	6
Total	5	8	1	14	***15	***0	0	15

Statistical results refers to left vs right eye exposition. * = .07 $< p <$ .05, ** = .05 $< p <$ .01, *** = $p <$ .01

observed the same pattern when considering the eye that lizards exposed once stopped in order to monitor the predator (Table 2). Finally we recorded what happened after the third stimulation. A total of 8 left eye-patched lizards exposed their right eye, whereas 5 lizards exposed the patched left eye (Binomial test, $p = .157$; Table 1). One lizard exposed the back. All 15 individuals with the patch on the right eye exposed the left eye towards the predator (Binomial test, $p < .001$; Table 1). Focusing on the eye exposed during stops, we observed similar results (Table 2).

After stimulation, lizards C-bent their body 27 times at the beginning of the flight. Out of 27 times this was performed 18 times by left eye-patched lizards and 9 times by right eye-patched lizards (Binomial test, $p = .03$). The C-bending was carried out 12 times by females and 6 times by males (Binomial test, $p = .071$). C-bending was carried out more quickly by left eye-patched lizards than by right patched ones (0.25 ± 0.08 s vs 0.68 ± 0.30 s; $U = 2.028$, $N = 27$, $p = .043$). Left eye-patched lizards C-bent 17 times anticlockwise and 1 time clockwise (Binomial test, $p < .001$). Right eye-patched lizards C-bent 1 time clockwise and 8 times anticlockwise (Binomial test, $p = .018$). Anticlockwise C-bending was faster (0.22 ± 0.11 s) than clockwise C-bending (0.55 ± 0.20 s; $U = 2.256$, $N = 27$, $p = .024$).

DISCUSSION

Our results showed that right eye-patched lizards, i.e., lizards forced to use their left eye, were more efficient in responding to a predatory threat than lizards forced to use their right eye. After being threatened, the more adaptive response for a lizard would have been to expose the unpatched eye towards the predator in order to scrutinise the predator. After the first predatory threat, lizards that were frightened from the right side, i.e., lizards that were forced to observe the predator with their right eye, did not perform the test successfully. During the flight half of the animals exposed the covered rather than the uncovered eye towards the predator. In contrast, most of the right eye-patched lizards, i.e., lizards that were stimulated from the left side, carried out the test successfully, exposing the uncovered (left) eye towards the predator. Hence during the flight they could effectively monitor the approaching predator.

Therefore, according our earlier discussion, lizards that were forced to use their right eye during predatory threats seemed confused, and responded in a very inefficient way to a dangerous situation. A plausible interpretation of the behaviour of left eye-patched lizards is that they tried to use the covered left eye in order to monitor the predator. This would be consistent with the known evidence on the dominant role of the right hemisphere in controlling fear reactions to predatory threats.

We did not find any difference in flight latency between left and right eye-patched individuals, although there was a tendency in right eye-patched lizards to show shorter latency after all three stimulations. The great inter-individual variability of flight latency could have prevented the emergence of significant differences, as shown instead in other species, which revealed an advantage of the left eye (right hemisphere) in latency of predator detection (e.g., Rogers, 2000).

At the beginning of the flight lizards sometimes showed a body C-bend behaviour. Although the motor commands for escape behaviour in C-bending could be ballistic (i.e. under solely motor control), sensory information is necessary to coordinate a successful escape behaviour before the beginning of the motor sequence (Eaton & Emberley, 1991). In frontally stimulated fish C-bending may mean monitoring of the frightening stimulus with the eye that remains external during the C-shaped movement. Thus a clockwise C-bend would indicate a left-eye predator monitoring before escaping; conversely, an anticlockwise C-bend would indicate a right-eye monitoring before escaping (Cantalupo, Bisazza, & Vallortigara, 1995). However, when the stimulus comes laterally the direction of C-bending is usually highly correlated with the direction from which the stimulus arrives (Canfield, 2007; Domenici & Blake, 2003).

It would be extremely disadvantageous to start responding with the uncovered eye and then turn the body to expose the covered eye during the flight. Lizards with the patch on the left eye (and thus threatened from the right side), responded by trying to expose the left eye—the one they use most frequently in the predatory context (Bonati et al., 2010)—C-bending with high frequency and speed. However, they had their left eye patched and their behaviour would thus not be convenient or advantageous. This could explain why, in contrast, lizards with their left eye uncovered, and the possibility of using it immediately, were slower in changing eye (in fact they C-bent much less frequently).

In conclusion, our study shows that lizards allowed to use only their left eye react better in antipredatory contexts than those allowed to use only their right eye. This fits with independent evidence, both in the laboratory and in the field, for a left eye mediation of predatory inputs (Bonati et al., 2010; Martín et al., 2010). Moreover, in conjunction with the novelty of using a monocular occlusion technique, this is the first report of laterality in C-bend behaviour in lizards, in strictly controlled laboratory conditions. Our results therefore support the hypothesis of a specialisation of the right hemisphere (mainly served by contralateral left eye structures) in response to predatory threat in the *Podarcis muralis*.

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