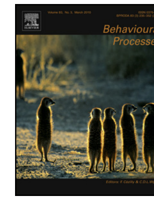
Behavioural Processes 97 (2013) 80–83

Contents lists available at SciVerse ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc



Advantages in exploring a new environment with the left eye in lizards

Beatrice Bonati[a,*], Davide Csermely[a], Valeria Anna Sovrano[b,c]

[a] Dipartimento di Bioscienze, Museo di Storia Naturale, Università di Parma, via Farini 90, 43121 Parma, Italy
[b] Dipartimento di Scienze della Cognizione e della Formazione, Università di Trento, Corso Bettini 31, 38068 Rovereto, TN, Italy
[c] CIMeC, Centre for Mind-Brain Sciences, University of Trento, Corso Bettini 31, 38068 Rovereto, TN, Italy

ARTICLE INFO

Article history:
Received 28 November 2012
Received in revised form 18 March 2013
Accepted 1 April 2013

Keywords:
Lateralisation
Exploratory behaviour
Lizard
Monocular test
Podarcis muralis
Visual asymmetry

ABSTRACT

Lizards (*Podarcis muralis*) preferentially use the left eye during spatial exploration in a binocular condition. Here we allowed 44 adult wild lizards to explore an unknown maze for 20 min under a temporary monocular condition whilst recording their movements, particularly the direction of turns made whilst walking within the maze. Lizards with a patch on their right eye, i.e. using their left eye to monitor the environment, moved faster than lizards with a patch on their left eye when turning both leftward and rightward in a T-cross. Hence, right eye-patched lizards were faster than left eye-patched lizards also in turning right, although their right eye was covered. Thus, lizards that could use the left eye/right hemisphere to attend spatial cues appeared to have more control and to be more prompt in exploring the maze. In addition, female lizards with their left eye covered stopped very frequently when they reached crosses, showing a high level of indecision. Results confirm that *P. muralis* lizards using their left eye only in exploring a new environment react faster and more efficiently than those using the right eye only in exploration. Hence lateralisation of spatial stimuli mediated by the left eye/right hemisphere could provide an advantage to this species.

1. Introduction

We know that behavioural biases associated with brain asymmetries are widespread in vertebrates (MacNeilage et al., 2009; Vallortigara et al., 2011), as well as in invertebrates (Rogers and Vallortigara, 2008; Frasnelli et al., 2010, 2012; Anfora et al., 2011; Rigosi et al., 2011). There is evidence that being lateralised could be beneficial (Güntürkün et al., 2000; Rogers, 2000; Rogers et al., 2004), and could increase the fitness of individuals (Ghirlanda and Vallortigara, 2004; Vallortigara and Rogers, 2005; Ghirlanda et al., 2009). Having a specialised brain, in fact, may enable the simultaneous performance of dual tasks, which can be processed in parallel (Rogers et al., 2004; Güntürkün et al., 2000). In many instances, indeed, lateralised individuals perform dual tasks better than non-lateralised individuals (fishes: Dadda and Bisazza, 2006; pigeons: Güntürkün et al., 2000; chicks: Rogers et al., 2004; cats: Fabre-Thorpe et al., 1993).

The presence of lateralisation is most typically manifested in the form of preferences in eye use in animals with laterally placed eyes, the complete cross-over of optic nerve fibres and reduced inter-hemispheric communication (Vallortigara et al., 1999). Such preferences have been observed both in the laboratory (e.g. Sovrano et al., 1999) and in the wild (e.g. Ventolini et al., 2005; Martín et al., 2010).

Several studies suggest that learning the topography of an environment is lateralised and associated with a left-eye bias due to the predominant right hemisphere control (Tommasi et al., 2003; Sovrano et al., 2005). Recent studies have revealed behavioural lateralisation in the common wall lizard (*Podarcis muralis*) for exploratory behaviour (Bonati and Csermely, 2011; Csermely et al., 2011). In particular, Csermely et al. (2011) found a bias in lizards with regard to the preferential use of the left eye during the exploration of a maze under laboratory conditions. However, the evidence collected so far concerns biases in spontaneous eye use during binocular viewing, as revealed by turning behaviour. Here we attempted to use a technique of temporary occlusion of the left or right eye during exploratory behaviour. Such a technique was recently used for the first time in lizards to study responses to a simulated predator threat (Bonati et al., in press). Here, the same technique is used in order to evaluate exploratory behaviour in a maze. We expected that lizards would move and turn in the maze more rapidly when using their left eye only than when using their right eye only.

Abbreviations: LTT, left T-turn; RTT, right T-turn; LLT, left L-turn; RLT, right L-turn; LLS, left L-straight; RLS, right L-straight.

* Corresponding author. Tel.: +39 0521 033406; fax: +39 0521 347002.
E-mail addresses: beatrice.bonati@unipr.it (B. Bonati), csermely@unipr.it (D. Csermely), valeriaanna.sovrano@unitn.it (V.A. Sovrano).

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http://dx.doi.org/10.1016/j.beproc.2013.04.002

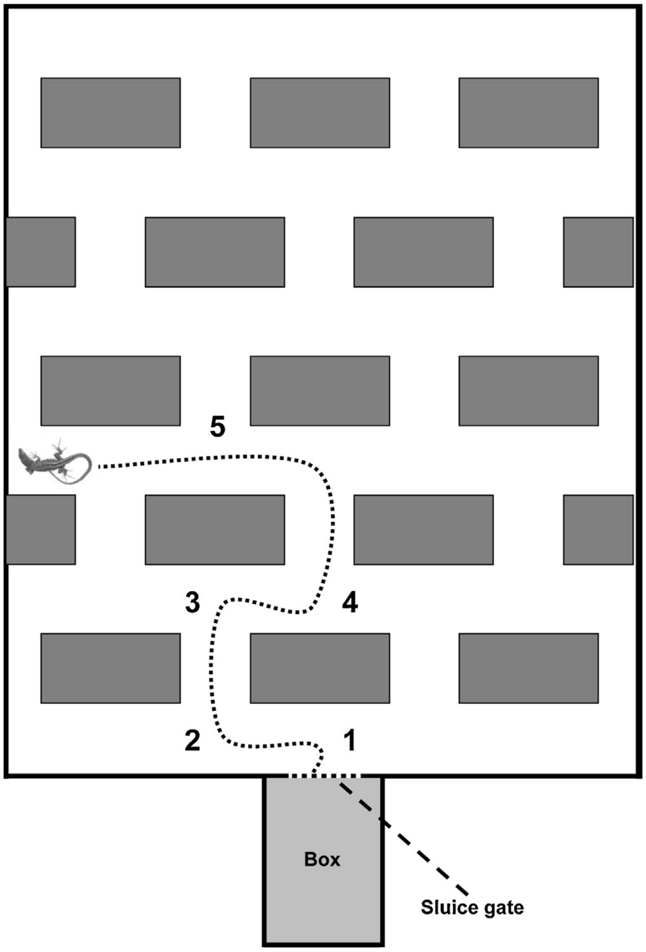

Fig. 1. The maze used for tests (from Csermely et al., 2011, modified). Type of turns we considered for behavioural analyses: 1 = left T-turn (LTT); 2 = right L-turn (RLT); 3 = right T-turn (RTT); left L-turn (LLT); right L-straight (RLS).

2. Materials and methods

By noosing, we collected 44 adult common wall lizards (*P. muralis*), 25 females and 19 males, from April to September 2011. Lizards came from scattered populations within Northern Italy. Once captured, the animals were put in cloth bags and carried to the laboratory, where they were maintained in 49 × 29 × 25 PVC cages, with sand substratum and some rocks for hiding and basking, under natural Italian spring–summer photoperiod and temperature (25–35 °C). They were fed daily with mealworm larvae (*Tenebrio molitor*) and water ad libitum. The lizards were maintained in these conditions without any manipulation for 24 h to become accustomed to captive conditions (cfr. Braña, 2003).

Before testing, lizards were individually eye-patched. The eye-patch consisted of a piece of opaque cotton cloth, which was dimensionally different for each individual lizard in order to fit the area around the eye. The patch was settled with commercial glue (Bostik®), which is totally harmless for horny lizard skin as it is frequently renewed. The glue was spread carefully on the area around the eye with the help of a wooden toothpick just before placing on the patch. We patched the left eye of 9 males and 14 females, and the right eye of 10 males and 11 females. These lizards were maintained individually for 24 h in an empty cage to become accustomed to the eye-patch condition.

At testing, each lizard was placed into a carton box 15.0 cm × 9.0 cm × 6.5 cm located at the entrance of the maze. The maze consisted of a 54.0 cm × 66.0 cm × 6.5 cm PVC arena (Fig. 1) containing thirteen 12 cm × 6 cm × 6 cm plastic blocks placed in a chequer design in the middle of it and four 6 cm × 6 cm × 6 cm plastic blocks placed against the sides, to maximise the number of "T" crossings. Since the blocks were rough and easily climbed by lizards they were covered with a smooth adhesive sheet to prevent this. The maze was covered with a transparent Plexiglas panel. After 5 min of habituation to the novel environment, the experimenter remotely lifted the front door of the box by pulling a thin cable from behind a blind and the lizard was free to enter the maze. The test started when the lizard entered the maze and ended 20 min later. During the test, the lizards moved freely along the maze aisles. Each lizard was tested once. When the test ended, the lizard was returned to its home cage and the eye-patch was spontaneously removed within a few hours; the next day each lizard was released at the site of capture. Overall, each lizard remained in captivity for up to 10 days. No animal was harmed as a result of testing.

All tests were recorded with a digital mini DV colour video camera 17.0 cm × 9.0 cm × 8.0 cm, which was placed above the maze on a tripod at a height of 180 cm. Frame by frame analysis of the test files was possible by using the Virtualdub™ video software.

We considered two types of cross for analyses: "T-cross", i.e. where the lizard had the binary choice of turning left or right, and "L-cross", where the lizard had the binary choice of turning left/right or going straight (Fig. 1). We considered the following behavioural parameters in both left and right eye-patched lizards: (1) the frequency and the duration of left T-turns (LTT) and right T-turns (RTT), i.e. the number and the time of turning of left and right turns when the lizard reached a T-cross (Fig. 1); (2) the frequency and the duration of left L-turns (LLT) and right L-turns (RLT), i.e. the number and the time of turning of left and right turns performed by the lizard when reaching to an L-cross (Fig. 1); (3) the frequency and the duration of left L-straights (LLS) and right L-straights (RLS), i.e. the number of times that the lizard choose to go straight when reaching to an L-cross (Fig. 1) and the time they needed to do it; and (4) the frequency and the duration of stops before an LTT or RTT.

The data were analysed with the PASW Statistic 18.0 for Windows software (SPSS, 2011). We used the Chi-Square test (χ^2) to compare the frequencies of first turn and the Mann–Whitney *U* test (*U*) to compare both the turn frequencies and the turn durations. Moreover, we also used the Mann–Whitney *U* test (*U*) for analysing the turn frequency for lizard per test to make a comparison with the data from the study by Csermely et al. (2011). Means are ±SE and the probability, set at $\alpha = 0.05$, is two-tailed throughout.

3. Results

3.1. T-crosses

3.1.1. Frequencies

Once in the maze, lizards explored the new environment and no animal tried to return into the initial box. The number of T-turns per lizard per test was 6.23 ± 0.89. Comparing the total frequency of turns of the present lizards with the total frequency of turns made by unpatched lizards, studied by Csermely et al. (2011), we found that patched lizards moved less (6.23 ± 0.89 vs. 15 ± 2.33; $U = 4.072$, $N = 65$, $P < 0.001$). The first turn made in the maze was a T-turn. Five out of 23 left eye-patched lizards made the first T-turn to the left whereas the remaining 18 lizards to the right ($\chi^2 = 7.348$, $N = 2$, $P = 0.007$). Among the 21 right eye-patched lizards, 16 made the first turn to the left (16 vs. 5; $\chi^2 = 5.762$, $N = 2$, $P = 0.016$). When faced with a T-turn, left eye-patched lizards made 2.52 ± 0.69 LTTs and 3.00 ± 0.74 RTTs ($U = 0.811$, $N = 46$, $P = 0.417$). Right eye-patched lizards turned 3.76 ± 0.86 times to the right and 3.24 ± 0.74 times to the left ($U = 0.408$, $N = 42$, $P = 0.683$). No difference was found

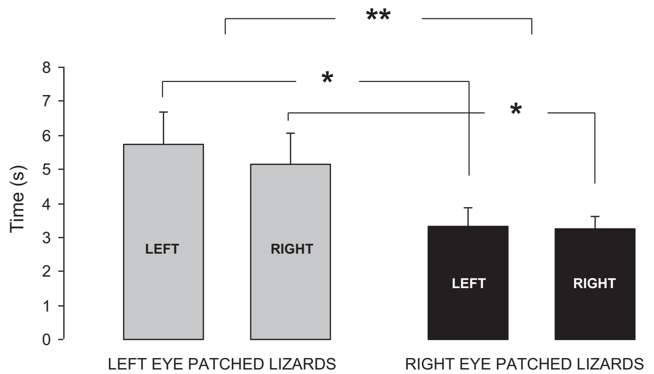

Fig. 2. Duration of left and right T-turns, respectively, in left and right eye patched lizards. $^{*}P < 0.05$, $^{**}P < 0.01$.

comparing left and right frequencies of T-turns between left and right eye-patched lizards ($U = 1.025$, $N = 88$, $P = 0.305$). When examining the stops before T-turns, we found that left eye-patched males never stopped before turning left whereas left eye-patched females stopped 7 times. Left eye-patched males stopped once before turning right whereas left eye-patched females stopped 10 times. Conversely, right eye-patched males stopped twice before turning left and 5 times before turning right, and right eye-patched females stopped 3 times before both turning left and right.

3.1.2. Durations

Left eye-patched lizards made an LTT in 5.74 ± 0.96 s and an RTT in 5.16 ± 0.90 s ($U = 0.489$, $N = 26$, $P = 0.625$; Fig. 2). Right eye-patched lizards had an LTT time of 3.32 ± 0.54 s and an RTT time of 3.24 ± 0.37 ($U = 0.024$, $N = 27$, $P = 0.981$; Fig. 2). We found a difference in the comparison of durations of left eye-patched vs. right eye-patched lizards for both LTTs ($U = 2.042$, $N = 27$, $P = 0.043$; Fig. 2) and RTTs ($U = 1.957$, $N = 26$, $P = 0.050$; Fig. 2); consequently a significant difference between left and right eye-patched lizards was found in T-turn durations (both left and right together; $U = 2.751$, $N = 53$, $P = 0.006$; Fig. 2). We did not find any difference in any kind of stops.

3.2. L-crosses

3.2.1. Frequencies

In left eye-patched lizards, the number of LLTs was 2.74 ± 0.59 and the number of RLTs was 3.43 ± 0.63 ($U = 0.968$, $N = 46$, $P = 0.333$). In right eye-patched lizards, we recorded 3.81 ± 0.89 LLTs and 3.48 ± 0.72 RLTs ($U = 0.025$, $N = 42$, $P = 0.980$). Comparing lizards with the left eye patched vs. lizards with the right eye patched, we did not find any difference ($U = 0.679$, $N = 88$, $P = 0.497$). Then, we analysed the number of times that lizards went straight when faced with an L-cross. Left eye-patched lizards went straight 3.39 ± 0.62 times in a left L-cross and 2.74 ± 0.68 times in a right L-cross (LLS vs. RLS; $U = 1.092$, $N = 46$, $P = 0.275$). In right eye-patched lizards, we observed 3.62 ± 0.75 LLS and 3.71 ± 0.65 RLS ($U = 0.292$, $N = 42$, $P = 0.770$). No difference emerged comparing left vs. right eye-patched individuals in LLS and RLS frequencies ($U = 0.835$, $N = 88$, $P = 0.403$).

3.2.2. Durations

Left eye-patched lizards made an LLT in 3.02 ± 0.47 s and an RTT in 3.20 ± 0.43 s ($U = 0.284$, $N = 32$, $P = 0.776$). Right eye-patched lizards had an LLT time of 3.10 ± 0.25 s and an RLT time of 2.49 ± 0.26 ($U = 1.882$, $N = 31$, $P = 0.060$). We did not find any difference in the comparison durations of left eye- vs. right eye-patched in both LLT ($U = 0.707$, $N = 30$, $P = 0.480$) and RLT ($U = 1.192$, $N = 33$, $P = 0.233$).

4. Discussion

The results showed that common wall lizards using their left eye to explore a maze were faster and made less stops than those using their right eye. We interpret this as less hesitation and as evidence that the right hemisphere (mainly served by the left eye) is predominantly attending to spatial cues. Differences were found only for T- and not L-crosses. This is likely due to the fact that T-crosses were the only locations where individuals had to make a real left-right binary choice (see Fig. 1).

A left eye bias in attending to spatial cues has been previously reported in lizards: Csermely et al. (2011) found that individuals moving freely in a maze strongly and steadily preferred turning to the left when facing a T-cross. The present results with animals tested under monocular conditions confirmed that the bias is likely to be the consequence of visual system asymmetry. As expected, eye occlusion made lizards less confident during exploration, reducing their overall movements within the maze. If we compare the total frequency of turns made by lizards using both eyes studied by Csermely et al. (2011) and the total frequency of turns made by our patched lizards, such an effect is apparent.

Once they had entered the maze, most of the lizards with their left eye patched made the first turn (a T-turn type, Fig. 1) to the right, whereas most of lizards with their right eye patched turned left. Lizards that were allowed to use both eyes in the study by Csermely et al. (2011) turned to the left without exception, indicating a preferential use of the left eye. Here, conversely, the lizards made the first turn to the side of the non-obstructed eye, as expected. Later on, both left and right eye-patched lizards that could use the left eye made subsequent turns (both T and L) with the same frequency to the left and to the right, indicating a successful habituation of the free left eye to control both the left and the right side of the space, and showing how the free (not patched) eye was used for turning both left and right. We believe that this is the reason why any difference in turn frequencies was found. A higher number of females than males (just one), when in front of a T-cross again, made stops before turning. To stop before turning in T-crosses, when the choice is to go left or right, may indicate indecision about what to do, highlighting vacillation before moving. The presence of stops recorded principally in females would indicate two possible hypotheses: a greater fearfulness in females or a difference in lateralisation between sexes. However, the latter hypothesis implies a difference also in turning, which we did not record. As *P. muralis* males are territorial, the stronger motivation to territoriality brings left eye-patched males to monitor and defend their area, leading them to explore and to move more in a new environment. The opposite was seen for left eye-patched females. Stops before T-turning were also made by some right eye-patched lizards; however, the latter stopped less and without variability between sexes and individuals.

The most interesting finding of the study concerned the time of turning. We found that lizards that could use their left eye were faster in T-turns than those with their left eye patched (Fig. 2). As we did not observe any difference in left T-turn vs. right T-turn duration within groups (i.e. into the left and into the right eye-patched lizards), but between groups only, it seems likely that the eye use is crucial for making decisions, which results in the difference seen. If individuals can explore using their right eye only, they turn slowly; conversely, if they can explore using the left eye only, their performance improves greatly in terms of decision time. This result is independent of the direction of the turn. In fact, lizards with the left eye free appeared faster both in left and in right T-turns than left eye-patched lizards, again suggesting the crucial role of the eye used. Consequently, it is reasonable to not find any differences in the frequency of direction of turns, as recorded in both left- and right eye-patched individuals. The only eye that lizards could use allowed them to move indifferently to the left or to the right (with equal frequency), but with a different performance and outcome that depended on which eye was available. In contrast, non-patched lizards used in the study by Csermely et al. (2011) either eye to observe the environment at T-crosses; hence, they could freely manifest their preferential side bias, moving towards the direction of the real preferential view. The specialisation of the left eye to explore, hence, could give the advantage of higher speed of spatial cues perception, which enables the lizards to be faster and more confident when exploring new environments. Moreover, less indecision and less vacillation during the exploration could also allow individuals to be prompt when facing any sudden threat, especially in a new, unknown environment. Having a specialised, i.e. asymmetric, brain would provide, therefore, crucial benefits for survival in *P. muralis*, which explains why, in this species, lateralisation is so widespread and strong, in particular with regard to exploratory behaviour (Bonati and Csermely, 2011; Csermely et al., 2011).

In conclusion, our results confirm the left eye/right hemisphere dominance in the control of exploration and navigation in *P. muralis*. In particular, our data support the hypothesis that lizards presenting such a specialisation obtain considerable advantages in everyday behaviour, thus supporting the idea that lateralisation increases individual brain efficiency (Vallortigara and Rogers, 2005).

Acknowledgements

We thank Giacomo Sciacca for his helpful collaboration in performing the tests. This study was supported by the Italian Ministero dell'Istruzione, Università e Ricerca and by a grant from the Comune di Rovereto to DiSCoF, University of Trento, to B.B.

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