Review

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

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ABSTRACT

Lateralization in ectotherms is now as well studied as in endotherms. Bias in eye use seems widespread, particularly in several ectotherms, most of them having lateral eyes. Several studies evidenced that the right eye/left hemisphere is involved in predatory behaviour and food searching while the left eye/right hemisphere seems to control predator monitoring, making lateralized individuals able to carry out both tasks simultaneously. Starting from previous observations that demonstrated a right-eye/left-hemisphere preference for observing a prey in common wall lizards, *Podarcis muralis*, we investigated whether a visual lateralization in antipredatory behaviour is present too. In a first experiment, we induced lizards in a terrarium to escape from a simulated predator attacking from behind, recording the direction of the escape path in relation to the starting point. We found that the preferred escape direction of most lateralized individuals was to the right and there was also a strong rightward preference in escape direction as a whole. In a second experiment the lizards, again stimulated from behind, had to choose to run down either the right or the left arm of a semi-circular tunnel ("ram-horn" maze). The rightward preference in escape behaviour was confirmed in this experiment too. We conclude that the constant rightward escape could be due to a left-eye early perception of the threatening cue and to the possibility it gives of better monitoring of most of the terrarium surface. Moreover, we found a left bias in turning the head for monitoring the predatory stimulus during escape, supporting the hypothesis that such a preference is likely due to visual lateralization rather than to motor lateralization.

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Contents

1. Introduction

Initially attributed to mammals and birds only, nowadays lateralization is as well known in ectotherms as in endotherms, indicating its possible common ancestral origin in vertebrates [26]. There is indeed evidence of anatomical asymmetries in ectotherms, also implying behavioural bias. In particular, as most ectotherms are lateral-eyed animals, the persistent observation of a stimulus is largely supported by a monocular visual field, inducing a left-/right-side choice that could be guided by laterality [37]. Actually, asymmetries in eye use seem widespread in lateral-eyed animals [39].

Dharmaretnam and Andrew [14] first observed how different patterns of eye use were elicited by different stimuli perceptions in the domestic chick. Several subsequent works confirmed this observation in other taxa too, supporting the hypothesis that lateral asymmetry could be task and stimulus dependent [37,36]. This brain-side specialization could induce the advantageous possibility of making more behavioural survival tasks simultaneous, processing and elaborating each one with one or other hemisphere [28,31,12]. The advantage has been shown, for example, in lateralized *Gallus g. domesticus* chicks that, in the presence of a predator model, perform better than non-lateralized chicks in both pecking food and vigilance [31].

In particular, the left hemisphere has been found to be involved in patterns required to focus the stimulus in salient cues important for survival, such as predatory behaviour and food searching [23,20,11]. For example, when foraging, *Podarcis muralis* lizards in a T-maze prefer looking at the prey with the right eye, processing the predatory input perception with the left hemisphere [7].

In contrast, the right hemisphere seems to control rapid responses to any changes in immediate surroundings [2]. Conspecific aggression, exploration and predator monitoring are then expected to be guided by the left eye [13,27]. Several bird species prefer monitoring the predator with the left eye [17,21,28]. Toads are more reactive in escaping from a predator appearing from the left monocular visual field than from the right one [22].

Cantalupo et al. [9] found immature and adult *Girardinus falcatus* fish to be lateralized to turn rightward in a C-start pattern during escape behaviour in initial session presentations when in front of a simulated predator. Although the motor commands for escape behaviour in C-bending behaviour could be ballistic (i.e. under motor control), sensory information is necessary to coordinate the successful run before starting [16]. Thus, a rightward C-start would be indicative of a left-eye predator control before and during escape [9]. Dill [15], instead, considered lateralization in escape behaviour as the result of a motor performance only. Measuring the escape angle, he found a "handedness" in the Pacific tree frog (*Hyla regilla*) for jumping to the left-hand side when facing a suspended rubber ball coming in front of it [15].

There is no information about lateralization in antipredatory behaviour in sauropsids. Cooper [10] showed that the escape behaviour from a simulated predator in the lizards *Sceloporus virgatus* and *S. jarrovii* is performed with higher success if they can monitor the predator. During the escape, these lizards also stop and turn their heads, controlling the predatory stimulus. As common wall lizards, *P. muralis*, show a visual lateralization in observing prey cues [7], we aimed here to investigate their antipredator-escape behaviour, to ascertain the possibility of a visual and motor lateralization in monitoring and in running while escaping from a predator. We expected that, according to the left-eye vigilance hypothesis, lizards monitored the predator stimulus with the left eye during the escape stops.

2. Materials and methods

In June 2008 we collected, by noosing, 21 adult *P. muralis* lizards (11 females and 10 males) from rock walls at a high mountain population ("Puerto de Navacerrada", Guadarrama Mountains, central Spain) in June 2008. Lizards were maintained at "El Ventorillo" Field Station, 5 km from the capture site, in PVC cages (49 cm × 29 cm × 25 cm) with a vermiculate substratum and some rocks for hiding. Lizards were fed mealworm larvae (*Tenebrio molitor*) daily and water was provided *ad libitum*. Photoperiod and temperature were both natural, i.e. those of the surrounding region, and regulated with artificial lighting. Lizards stayed in captivity for at least a week to acclimatize to laboratory conditions before the experiments were started. At the end of the experimental period, lizards were released at the capture site. None of the lizards was harmed during the tests. Lizards were captured under licence from the "Comunidad de Madrid" Environmental Agency.
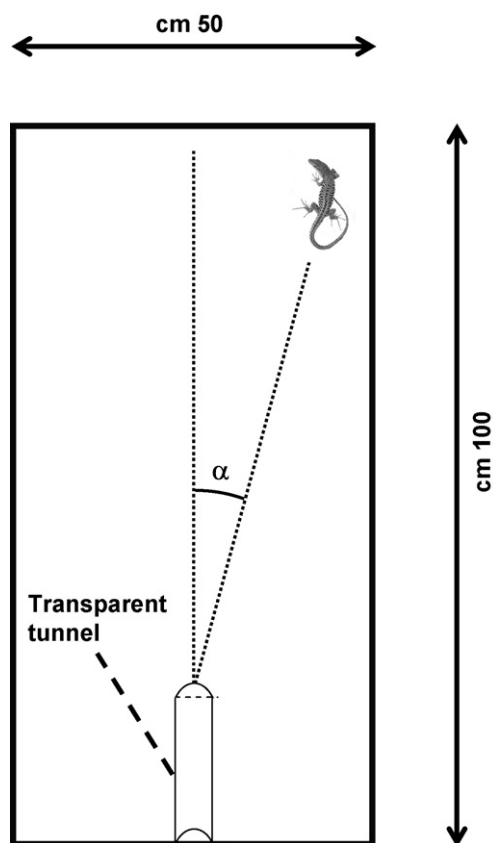

Fig. 1. The experimental apparatus used in experiment 1.

2.1. Experiment 1

Before the beginning of trials, we allowed lizards at least 2 h to thermoregulate and attain a temperature allowing maximal locomotor performance, necessary to express correct escape behaviour. At testing, the lizards were placed individually in a 100 cm × 50 cm × 50 cm glass terrarium (Fig. 1) with a polystyrene floor that provided excellent traction for running. No cover was added. A transparent PVC cylindrical tunnel (20 cm long, 5 cm in diameter) (Fig. 1) was placed in the middle of the proximal short side of the terrarium to both induce the lizard into having its body axis aligned with the tunnel's longitudinal axis when getting out of the tunnel (i.e. at the beginning of the escape), and to avoid injuring lizards during stimulation. All the terrarium's walls were covered with opaque polystyrene panels to avoid external stimuli influencing the lizard's choice of escape direction.

During tests, the observer stayed at the back of the apparatus, gently put the lizard into the tunnel and then immediately stimulated it with a brush (21 cm × 3.5 cm × 1 cm) in order to induce the escape. The stimulation was made by beating the brush on the tunnel, simulating a predator attack, and was done by the same experimenter in a standardized way using the right and left arm, alternately, to eliminate the possibility of an influenced choice of direction. The stimulation was then auditory without a tactile stimulus on the lizard. The test started when the lizard arrived at the end of the tunnel and escaped freely within the terrarium, and was ended when the lizard touched one of the terrarium walls with its body. If the lizard stopped running before reaching any wall of the terrarium, the experimenter beat the tunnel with the brush again. The lizard sometimes froze before completing the test, without arriving at the end of the terrarium, regardless of repeated stimulations. In such cases the test ended at the lizard's last stop.

Lizards were recorded continuously using a digital event recorder. Lizard behaviours considered during the test were: (1) the direction and angle of escape, calculated in relation to the longitudinal axis of the tunnel (see below), (2) the direction of head rotation when stopping during the escape run, and (3) the number of stops with head rotation during the run. All tests were recorded with a mini DV colour JVC GR-DVL365EG video-camera, 17 cm × 9 cm × 8 cm in size, placed on a tripod 150 cm above the terrarium floor.

The video software, Virtualdub (www.virtualdub.org), permitted frame-by-frame videotape analysis. The escape angles were measured on printed videotape snapshots. We drew a line starting from the midline of the tunnel at its end to the lizard's neck. The angle was calculated with a goniometer referring to the longitudinal tunnel axis (0°). Angles to the left- or to the right-hand side of that axis were measured, considering both the lizard's first stop position (initial escape angle [IEA])
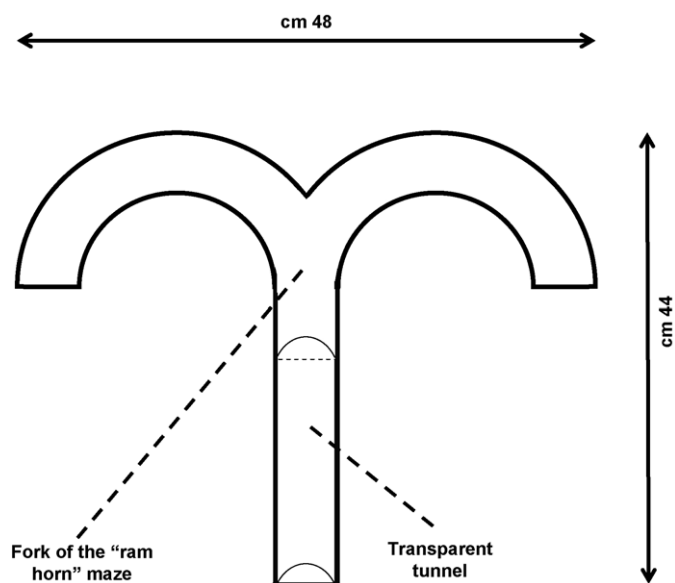
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Fig. 2. The "ram-horn" maze used in experiment 2.

Table 1
Number of tests carried out in experiment 1 when lizards escaped with a straight run (without lateral preference) or to the left or right direction from the tunnel longitudinal axis. The probability, obtained by binomial test, refers to the comparison of left- and right runs, and is followed by the laterality index (LI) for each individual. Lizards are ordered for the LI value.

Lizard	Straight run	Left run	Right run	p	LI
1	0	1	9	0.010	0.90
2	1	1	8	0.018	0.89
3	2	1	7	0.031	0.86
4	0	2	8	0.044	0.80
5	0	2	8	0.044	0.80
6	2	2	6	0.109	0.75
7	0	3	7	0.117	0.70
8	0	3	7	0.117	0.70
9	0	3	7	0.117	0.70
10	0	3	7	0.117	0.70
11	1	3	6	0.164	0.67
12	1	3	6	0.164	0.67
13	1	3	6	0.164	0.67
14	0	4	6	0.205	0.60
15	0	4	6	0.205	0.60
16	0	4	6	0.205	0.60
17	1	4	5	0.246	0.56
18	1	4	5	0.246	0.56
19	0	6	4	0.205	0.40
20	0	6	4	0.205	0.40
21	3	6	1	0.055	0.14
Total	13	68	129		

and the position at the end of the test (final escape angle [FEA]). Due to the manual measuring error, which was estimated to be within 2°, the escape run was considered lateral only when the angle was greater than 2° to the left or to the right of the 0° line. To limit pseudo-replications, every lizard was tested twice daily maximum, with at least a 6 h inter-trial time, for a total of 10 days.

2.2. Experiment 2

In this experiment we used the same glass terrarium (100 cm × 50 cm × 50 cm) with a polystyrene floor and opaque walls, but we placed in the middle of the terrarium a "ram-horn" PVC maze (44 cm × 48 cm × 20 cm) without a floor and consisting of one straight central arm (30 cm × 5 cm × 20 cm) that led to two symmetrical semicircular lateral arms (14 cm × 5 cm × 20 cm) ("ram horns") (Fig. 2). The maze had no cover. Opposite to the fork leading to the semicircular lateral horns, the straight arm of the maze had a transparent PVC tunnel (19.8 cm long, 5.0 cm in diameter), which induced the lizard to align its body axis to the longitudinal axis of the tunnel when arriving at the fork. The presence of the tunnel also avoided injury to the lizard when it was stimulated with a brush (21 cm × 3.5 cm × 1 cm) to escape from the tunnel. The stimulation with the brush was made by the experimenter with the right and left arm, alternately, as above.

At the beginning of the trial, the observer stayed behind the apparatus, gently pushed the lizard into the tunnel and then immediately beat the tunnel with the brush, simulating a predator attack. The test started when the lizard arrived at the end of the tunnel and ended when it stopped the run, after passing the fork of the maze, i.e. after having chosen an escape direction. All tests were recorded with a mini DV colour video-camera as above, and later analysed frame by frame with the video software Virtualdub (www.virtualdub.org). To limit pseudo-replications, every lizard was tested twice daily maximum, with at least a 6 h inter-trial time, for a total of 10 days.

2.3. Data analyses

We used the binomial test, calculated with the web calculator "Easy calculation.com" (www.easycalculation.com), to analyse the running direction and the preference of maze lateral arm among individual lizards, and both the Chi-Square Component 'z' Index (z) [6] and the Wilcoxon Signed-Rank Test (T) to compare the sample's total choice frequency against the relative expected frequency for runs leftward and rightward and in either left or right arm, and for the lateral head rotation during the stops. We used the Mann–Whitney U-test (U) to compare angle values to the left and to the right.

For repeated tests of the same individual, we used a laterality index (LI) developed by Stancher et al. [35], calculated as: frequency of right runs/(total frequency of right runs + left runs) × 100. The LI was calculated for each subject that carried out more than one test to investigate possible lateralization at the population level and to compare the behaviour between sexes. Values of LI lower or greater than 50% indicate a left or right preference, respectively, while a 50% value indicated no preference. We used the one sample and two independent samples t-test (t) on the overall mean of the laterality indices. With the first test we evaluated a possible escape preference in a specific direction among the sample; with the second test we checked possible differences concerning the sexes. Both tests were also used to compare angle values. The Wilcoxon signed-rank test, the Mann–Whitney U-test

and the t-tests were calculated with the SPSS 15.0 for Windows® software [34]. Means are ±SE, and the probability, set at p = 0.05, is two-tailed throughout, unless otherwise stated.

3. Results

3.1. Experiment 1

The 21 lizards considered in this experiment usually escaped readily from the tunnel after the brush stimulation. We did not find any difference between IEA (5.08° ± 1.26) and FEA (4.97° ± 1.42) values (t(418) = 0.060, p > 0.05); consequently, we did not consider results other than for IEA values. Looking at the repeated tests as a whole (N = 210), the 21 lizards considered had an IEA of 16.8° ± 0.86 when escaping to the right and 16.0° ± 1.42 when escaping to the left (U = 1.206, N = 198, p > 0.05).

Focusing on the direction, lizards chose 129 times to escape to the right-hand side and only 68 times to the left-hand side (z = 3.073, p < 0.01), escaping on a path aligned to the tunnel axis 13 times only. The preference for the right direction in escape rather than to the left was confirmed by the LI calculation, which was highly significant (t(20) = 3.397, p = 0.001) for the whole sample. If we split the direction chosen by each lizard in the first test and in the remaining tests, we found that in 106 tests the lizards chose the same direction as they did in the first test, whereas in 70 tests the direction differed from that of the first test (z = 1.919, p < 0.05).

Females and males did not differ significantly in LI (t(19) = 0.040, p > 0.05). Six (28.6%) individuals out of the 21 tested were clearly lateralized because they showed a preference for the same escape direction in most of their tests: 9 from 10 (binomial test: p = 0.01), 8 from 9 (p < 0.05), 8 from 10 (p < 0.05), 8 from 10 (p < 0.05), 7 from 8 (p < 0.05), 1 from 7 (p = 0.05), respectively (Table 1). The direction chosen by these lateralized lizards was to the right for 5 lizards out of 6.

During the escape, all lizards stopped turning their heads to look back. During the stops, these lizards preferred rolling the head to the left-hand side than to the right-hand side (165 vs. 124 times, respectively; z = 1.705, p < 0.05). Five lizards in total had a bias for rolling their heads to the left more often than to the right: 17 from

23 times, 12 from 14, 12 from 16, 9 from 11, and 8 from 9, respectively (binomial test: $p < 0.05$ for all but one at $p < 0.01$). In more detail, all lizards that rolled their heads preferred to do it to the left-hand side when escaping both to the left ($z = 1.732$, $p < 0.05$) and to the right ($z = 1.117$, $p < 0.05$). Moreover, when they escaped straight away, i.e. without choosing any preferential direction, again they rolled their heads more often to the left: 9 times against 2 times (binomial test, $p < 0.05$).

Analysing the first test only, 17 (81.0%) out of the 21 lizards escaped to the right, while only 4 (19.0%) escaped to the left (binomial test, $p < 0.01$). No lizard chose a straight-on direction, i.e. along the longitudinal axis of the tunnel. The mean angle to the right was $14.2° \pm 2.48$, a similar value to that to the left ($9.2° \pm 2.06$) ($U = 25.000$, $N = 21$, $p > 0.05$). During the escape, 9 lizards stopped looking back. During these stops the lizards significantly preferred turning their heads more often leftward than rightward (12 vs. 4 times, respectively; binomial test, $p < 0.05$). When lizards escaped from the tunnel to the left, they invariably rolled the head to the left-hand side during their stops (6 vs. 0 times, respectively; binomial test, $p < 0.05$). However, the 4 lizards that escaped from the tunnel to the right rolled their heads 6 times to the left and 4 times to the right (binomial test, $p > 0.05$).

3.2. Experiment 2

Sixteen of the 21 individuals considered attempted to escape to the right horn of the maze during their first test, while only 5 individuals attempted to escape to the left one (binomial test, $p = 0.01$). Considering the sex, 8 females chose the right horn while only 3 females chose the left one (binomial test, $p > 0.05$). The males behaved very similarly: 8 of them chose the right horn and only 2 chose the left one (binomial test, $p < 0.05$).

The 21 lizards were tested 10 times each, 210 tests in total. They escaped 126 times to the right horn and 83 times to the left horn ($z = 2.103$, $p < 0.01$). The preference to escape to the right horn of the maze was confirmed by the LI calculation ($t(20) = 3.246$, $p < 0.01$). In this experiment, too, we considered the outcome of the first test in relation to that in the subsequent ones. We found that in 101 tests the lizards chose the same horn as they did in the first test, whereas

in 87 tests the lizards did not choose the same horn as they did in the first test ($z = 0.722$, $p > 0.05$).

There was no sex bias in LI for the repeated tests ($t(19) = 0.542$, $p = 0.59$).

Each individual showed a variable preference for taking either horn of the maze; only 2 of them (1 male and 1 female) produced consistent responses, resulting then clearly lateralized (9 tests out of 10 for both; binomial test, $p = 0.01$). The direction of lateralization was to the right for both of them (Table 2).

4. Discussion

Our data from both experiments show that lizards, similarly to other taxa, are lateralized in their escape behaviour during a predator attack. Instead of running along a straight-on path, lizards showed a tendency to run to their right-hand side. The mean escape angle measured in experiment 1, in fact, showed that most lizards escaped by making a choice with respect to the longitudinal axis of the terrarium. The right- and left-angle similarity is indicative of a possible spontaneous tendency of lizards not to escape on a straight-on path from a predator, a behaviour that is likely to be an antipredator strategy. Escaping to the left or to the right, in fact, allows a greater possibility to modulate the withdrawal direction, avoiding a predator predicting the escape behaviour of a lizard.

Considering the first test carried out in experiment 1, most of the lizards escaped significantly rightward, and most of the individuals that were lateralized were biased for the rightward direction again. Despite the response displayed by those individuals, and the overall higher number of directions to the right in comparison to the left shown by most of the lizards, we suggest that the small percentage of lateralized lizards we found is likely due to the statistical sample size rather than an indication of absence of lateralization. The analysis of the population as a whole, in fact, revealed a rightward bias in LI, probably due to the bias tendency of each lizard for that direction (cf. Table 1).

The bias in rightward escape was confirmed in experiment 2, where the lizards had necessarily to choose a direction while running, without having the possibility to escape straight-on. This experiment allowed us to isolate the behaviour, strengthening the results of the other experiment. In this case, too, a right preference emerged both in the sample as a whole and among individual lizards, even if in a smaller number of lizards.

The type of lateralization we ascertained can be interpreted as the result of a pure ballistic reaction in response to a voluntary motor sequence, i.e. motor lateralization, or as a consequence of an early sensory perception that influenced the subsequent motor direction, i.e. sensory lateralization. If we consider the escape behaviour as the result of the ballistic reaction effect only, it is likely that the lizards ran to a preferred direction as an antipredator response that probably increases the success of the escape as a consequence of a high specific individual specialization in this task. Conversely, a bias for the same direction in the population may convey the specific disadvantage of the predictability of behaviour [38]. In our lizard sample, nevertheless, the escape angle measured in experiment 1 was protean, i.e. very variable, and the position of the lizard after the run caused by the stimulation was essentially unpredictable. Moreover, the presence in the population of non-lateralized or left-lateralized individuals could avoid a possible predator learning, as the result of a stable strategy [18,19]. Such a preference for a sideward path could be widespread among the vertebrates, because it has already been found for the escape behaviour in several fishes [9,5,23] and in the amphibian *H. regilla* [15].

Nevertheless, another hypothesis is that the lateralization in the escape behaviour we found is due to an asymmetry in sensory

Table 2
Number of tests carried out in experiment 2 when lizards escaped to the left- or to the right horn of the maze, the probability (binomial test) of the frequency difference, and the laterality index (LI) for each individual. Lizards are ordered for the LI value.

Lizard	Left horn	Right horn	p	LI
1	1	9	0.010	0.90
2	1	9	0.010	0.90
3	3	7	0.117	0.70
4	3	7	0.117	0.70
5	3	7	0.117	0.70
6	3	7	0.117	0.70
7	3	7	0.117	0.70
8	3	7	0.117	0.70
9	3	7	0.117	0.70
10	3	7	0.117	0.70
11	4	6	0.205	0.60
12	4	6	0.205	0.60
13	5	5	0.246	0.50
14	5	5	0.246	0.50
15	5	5	0.246	0.50
16	5	5	0.246	0.50
17	5	5	0.246	0.50
18	6	4	0.205	0.40
19	6	4	0.205	0.40
20	6	4	0.205	0.40
21	6	3	0.164	0.34
Total	83	126		

perceptions. In fact, although escape is a motor response, sensory visual information is necessary at the very beginning of the movement to successfully coordinate the escape, to know what and where the stimulus is, and where to flee [16]. When *Litoria palmate* tadpoles escape from an approaching aerial predator model, they too show a right-turning lateralization that is potentially attributed to motor asymmetries only, and is likely to be the result of a left-eye mediated visual lateralization, present in several anurans' larvae [29,40,27]. Prey species with lateral eyes, such as lizards, do not give any evident indication of detecting the predator until they flee, but its monitoring is likely to begin earlier than when they decide to escape [10]. In our case, a preferential escape direction could be indicative of an early perception, due to preventive single-eye monitoring. That perception brought individuals to escape to the opposite direction in relation to where the predator was actually perceived. In other words, escaping to the right might be the consequence of a left-eye control of the predatory cue. Moreover, running to the right side of the terrarium allowed monitoring a wider area for the use of the left eye, i.e. the central part of the terrarium in our experiment.

In addition, in experiment 1 we found a significant behavioural preference in left-turning the head towards the predator, in the stops during the run. This bias was found in the first test and was evident in the repeated tests too, regardless of whether the escape was rightward, leftward or straight-on. Moreover, the lateralized individuals for this task had a concordance in the direction, and the same left-preference emerged considering the sample as a whole. Movement discontinuity with alternation of active locomotion and frequent brief pauses is characteristic of lizard locomotion, even after threatening stimuli [4,3,8]. The functional significance of locomotor pause likely improves visual perception, increasing the probability of predatory perception [25,8]. An approach from behind requires the lizards, having lateral eyes and one single, central fovea in each [32], to turn their head or body to look at the predator [10]. The head turning to the left during those pauses in running could reveal a real preference in monitoring the predator during the escape, preferentially with the left eye.

Lippolis et al. [22] noted that in three *Bufo* species there was no apparent preference in left- or right-side jumping when presenting a simulated snake moving in their frontal field. Lippolis et al. [22] found, however, stronger escape and defensive responses when the snake moved in their left monocular visual field, indicating that preferences in evasive behaviour could likely be due to an asymmetrical eye use. Actually, left-eye perception for predatory cues and negative emotions are indicative of right-hemisphere control, as already reported in several taxa, such as fishes [9,5], toads [29,22], birds [30,21] and marsupials [24], but never in sauropsids. Such a bias in observing the predator with the left eye could be due to right-side brain structures involved in processing emotional responses, such as fear, as proposed by Koboroff et al. [21]. In fact, they found a strong left-eye preference in Australian magpies (*Gymnorhina tibicen*) before withdrawing from a real predator, but such a preference shifted to the right eye if the magpie did not display an alert posture when approaching the predator.

We did not find relevant differences between sexes in LI in either of the experiments. Some studies about the escape behaviour conducted in the same species did not find any intersexual difference in performing the escape behaviour [33,1,8]. Even so, in experiment 1 a consistent number of males appeared with a bias in escaping to a preferred direction. This trend could likely be explained with the stronger attitude of males to patrol the territory, as performed in the mating season.

In conclusion, in our two experiments we found in *P. muralis* lizards a form of lateralization for escaping rightward after a simulated predator attack from behind. This could be indicative of a preferential left-eye stimulus monitoring, supported by a left-head-turn preference towards the predator during the withdrawal. Our results, then, support the hypothesis of possible simultaneous control of important survival activities.

Acknowledgements

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