



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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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].

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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. jarrovi* 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 prey 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.

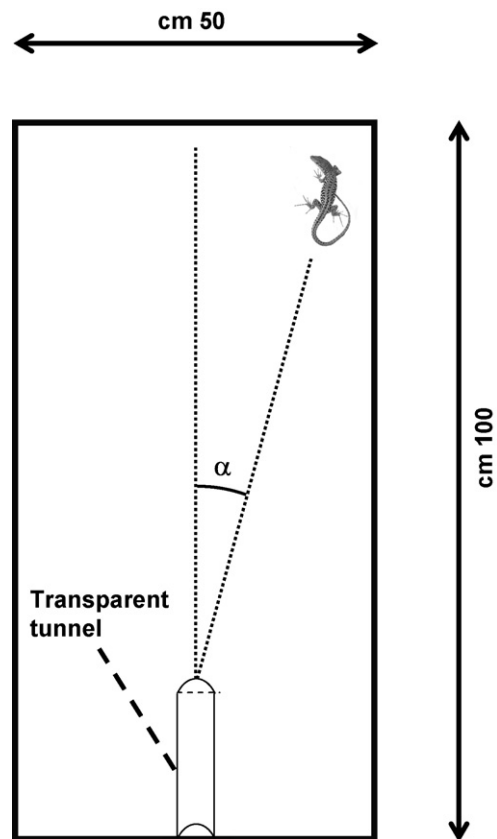


Fig. 1. The experimental apparatus used in experiment 1.

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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