

RESEARCH ARTICLE

Low-frequency electroencephalogram oscillations govern left-eye lateralization during anti-predatory responses in the music frog

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ABSTRACT

Visual lateralization is widespread for prey and anti-predation in numerous taxa. However, it is still unknown how the brain governs this asymmetry. In this study, we conducted behavioral and electrophysiological experiments to evaluate anti-predatory behaviors and dynamic brain activities in Emei music frogs (*Nidirana daunchina*), to explore the potential eye bias for anti-predation and the underlying neural mechanisms. To do this, predator stimuli (a model snake head and a leaf as a control) were moved around the subjects in clockwise and anti-clockwise directions at steady velocity. We counted the number of anti-predatory responses and measured electroencephalogram (EEG) power spectra for each band and brain area (telencephalon, diencephalon and mesencephalon). Our results showed that (1) no significant eye preferences could be found for the control (leaf); however, the laterality index was significantly lower than zero when the predator stimulus was moved anti-clockwise, suggesting that left-eye advantage exists in this species for anti-predation; (2) compared with no stimulus in the visual field, the power spectra of delta and alpha bands were significantly greater when the predator stimulus was moved into the left visual field anti-clockwise; and, (3) generally, the power spectra of each band in the right-hemisphere for the left visual field were higher than those in the left counterpart. These results support that the left eye mediates the monitoring of a predator in music frogs and lower-frequency EEG oscillations govern this visual lateralization.

KEY WORDS: Visual lateralization, Anti-predation, Visual field, Laterality index, Electroencephalogram, Power spectra

INTRODUCTION

Preferential use of one side of the body and cerebral lateralization, including hemispheric asymmetries in structures and functions, which ultimately result in differences at behavioral and physiological levels (Hellige, 1993), are well known in vertebrates and invertebrates (Frasnelli et al., 2012; Rogers et al., 2013). Hemispheric asymmetry may be demonstrated by the complexities in anatomy and neurons in diverse parts of each hemisphere, or differing levels of left/right motor ability (Concha et al., 2012; Franklin and Lima, 2001; Vallortigara and Rogers, 2020). The left hemisphere engages mainly in processing positive stimuli and learnt routine tasks, and responding to food or

prey; the right hemisphere is more associated with the responses to negative and unexpected stimuli or dangerous events (e.g. predators, conspecific aggression), and encoding the spatial relationships occurring in the surrounding environment (MacNeilage et al., 2009; Rogers et al., 2013). Substantial findings have shown benefits related to cerebral lateralization (Ferrari et al., 2017), such as specialization of certain cognitive or motor tasks by avoiding duplication of functions in the two hemispheres (Frasnelli, 2013; Vallortigara and Rogers, 2005), and processing several streams of information in parallel (Rogers et al., 2004; Vallortigara, 2006). However, it can result in some weaknesses; for example, the behavioral lateralization can be predicted by the predator (Vallortigara, 2006).

Visual lateralization, one of the brain specialization phenomena, is widespread in numerous vertebrates (Pellitteri-Rosa and Gazzola, 2018; Quresmini et al., 2014) and invertebrates (Romano et al., 2017; Schnell et al., 2018, 2016) when they process visual information. Generally, left-eye/right-hemisphere and right-eye/left-hemisphere preferences exist for identifying a predator or conspecific fight and identifying prey or food from other non-food items, respectively. The adaptive nature of such apparent hemispheric specialization might be correlated with optimizing predator vigilance with other tasks such as foraging (Franklin and Lima, 2001; Rogers, 2000) and social interactions (Dadda et al., 2003; Hews and Worthington, 2001). The preferential eye use for ecological activities is dependent on specialized function of the left or right brain (Rogers et al., 2013; Vallortigara et al., 1999). Consistent with this, our previous study indicated that dynamic electroencephalogram (EEG) oscillations, especially at higher frequencies, underlie the right-eye/left-hemisphere advantage in predatory behavior in the Emei music frog (*Nidirana daunchina*) (Shen et al., 2019). However, the underlying neural mechanisms of visual lateralization for anti-predatory behaviors are unclear.

In animals, anti-predatory behaviors are usually accompanied by continuously gathering information through their visual systems over a short period of time in order to make quick decisions to avoid predation for survival and reproduction (Fernández-Juricic, 2012; Hemmi and Zeil, 2005). This behavior may follow a series of steps to reduce the mortality rate in the event of a predator attack: scanning the context through a visual search, detecting the predator, identifying the predator right after detection, tracking it visually, and changing behavior to reduce visibility and/or escape (Cronin, 2005; Lima and Dill, 1990). Previous studies have shown that cognitive processes are governed via brain oscillations (Başar et al., 2001), which can be divided into several bands and might be involved in different brain functions, including sensory registration, perception (Romano et al., 2017), movement and cognitive processes related to attention, learning, memory and decision making (Başar et al., 2001; Mazza and Pagano, 2017). For example, our previous studies have shown that auditory perception in the music frog is closely linked to dynamic activities of diverse EEG bands (Fang et al., 2012b) and specific event-related potentials (Fan et al., 2019; Fang

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et al., 2015). In addition, because discrete brain regions are specialized for different cognitive functions (Kandel et al., 2013), it seems reasonable to hypothesize that eye preferences during anti-predatory behaviors might be associated with different activity patterns of specific EEG bands in specific brain regions.

In order to explore whether eye preferences exist in the music frog when it encounters a predator and how the visual central nervous system might govern such preferences, we investigated anti-predatory responses in this species at behavioral and electrophysiological levels. To do this, numbers of anti-predatory responses and power spectra of each EEG band were counted and analyzed, respectively, when a predator stimulus (a model snake head) was moved into the animal's left visual field (LVF) or right visual field (RVF). We predicted that (1) presentations of the predator stimulus in the LVF would elicit more anti-predatory responses compared with presentations in the RVF because the right hemisphere mediates fear and other emotional responses (Lippolis et al., 2002); (2) EEG power spectra in the right hemisphere would be higher than those in the left counterpart during anti-predatory responses because the optic nerve fibers decussate almost completely in the anuran visual system (Fite and Scalia, 1976; Rogers, 2002a), although a number of commissures may engage in inter-hemispheric communication (Halpern et al., 1968; Scalia, 1976); and (3) differences in power spectra in specific EEG bands would exist between the LVF and RVF because EEG bands interweave strongly with sensory and cognitive functions in the brain (Başar et al., 2001).

MATERIALS AND METHODS

Animals

During the breeding season, 47 adult music frogs [*Nidirana daunchina* (Chang, 1933)] (27 males and 20 females) were captured from the Emei mountain area (29.60°N, 103.36°E, 1315 m above sea level) of Sichuan, China. The frogs were separated by sex and housed in different opaque plastic tanks (45×35 cm and 30 cm high), which contained ~3 cm water and ~8 cm soil around the walls so that the animals could burrow and hide themselves. The tanks were placed in a soundproof room under a 12 h:12 h light-dark cycle (lights on at 08:00 h) with controlled temperature (23±1°C) and relative humidity

(70–80%). They were fed live crickets every 3 days. All frogs were used for the behavioral experiments, and 12 of them (six males and six females) were also used for the electrophysiological experiments. The mean mass and length (±s.d.) of the subjects was 8.6±1.2 g and 4.9±0.2 cm, respectively. The experimental procedures were approved by the Animal Care and Use Committee of Chengdu Institute of Biology and carried out according to international standards of animal care and use.

Surgery

Surgical procedures were similar to those described in our previous studies (Fan et al., 2019; Fang et al., 2012a; Yue et al., 2017). In brief, we anesthetized the animals deeply via a water bath with a 0.15% (0.0015 g ml⁻¹) solution of tricaine methanesulfonate (MS-222) and determined the optimum depth of anesthesia by the loss of the toe pinch response. After anesthesia, we implanted six cortical EEG electrodes, composed of miniature stainless steel screws (0.8 mm in diameter), inside each frog's skull and above both sides of the telencephalon (LT, RT), diencephalon (LD, RD) and mesencephalon (LM, RM), and implanted the reference electrode above the cerebellum (Fig. 1). We used dental acrylic to fix the electrodes on the skull. The animals were housed individually for 6 days for recovery before conducting further experiments. After all experiments were completed, we euthanized the animals with an overdose of MS-222 solution and confirmed the electrode locations by injecting Hematoxylin dye through the skull holes used for implanting the recording electrodes previously.

Behavioral testing apparatus

The testing apparatus was described in detail in our previous study (Shen et al., 2019). Briefly, a cylindrical cup (13 cm in height, 7 cm in diameter) made of transparent polymethyl methacrylate (PMMA) was hung in the middle of a U-shaped PMMA frame, and a white plastic wafer (22 cm in diameter) was adhered to the bottom of the cup for minimizing visual interference (Fig. 2). An electric turntable (5 cm in height, 20 cm in diameter) was placed beneath the cup, and its rotation direction and velocity could be controlled by a PC via WiFi. A PMMA bar was bent to form a right angle and adhered on a

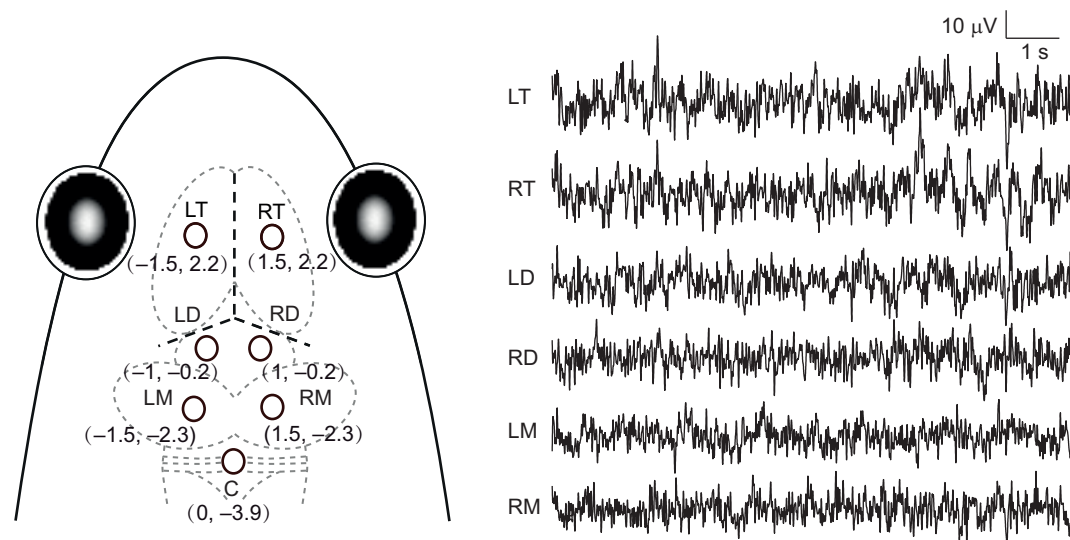


Fig. 1. Placement of electrodes on music frogs (*Nidirana daunchina*) and 10 s of typical EEG tracings for each channel in experiments. The intersection of the three bold dashed lines in the frog head denotes the intersection of suture lines corresponding to lambda. The numbers indicate the electrode coordinates with respect to lambda as the origin of coordinates. LT, RT, LD, RD, LM and RM denote the left and right sides of the telencephalon, diencephalon and mesencephalon, respectively; C denotes the reference electrode implanted above the cerebellum.

PMMA board on the electric turntable. All the components were surrounded by a white opaque plastic cylinder (30 cm in height, 40 cm in diameter). A video camera with infrared light source and motion detector (VSD-611H, Viesida Ltd, Shenzhen, China) was fixed on a tripod and positioned centrally ~ 1 m above the test apparatus to record behaviors of the animals.

Stimuli and test procedure

The head of a model of a snake (*Zaocys dumnades*), which distributes sympatrically with the music frogs, was used as a predator stimulus, and fresh leaves of similar size to the model snake head were used as the control. The head, with white eyes and red tongue, was $6 \times 2 \times 1.5$ cm, and was tethered using a white cotton thread and fixed to the end of the bar (Fig. 2). The distance between the stimulus and the cup containing the subject was maintained at ~ 2 cm.

The experiments were conducted in an electromagnetically shielded and soundproof chamber, during which the background noise, temperature, relative humidity and light intensity were maintained at 23.0 ± 1.7 dB, $24 \pm 1^\circ\text{C}$, 68–75% and 0.07 lx, respectively. Before the behavioral tests, the subject was placed in a cup containing water to a depth of ~ 1 cm, and the stimulus was moved behind the subject using the electric turntable. The stimulus circled the frog five times in a clockwise or anti-clockwise direction at a constant velocity of 2.4 revolutions min^{-1} (14.4 deg s^{-1}) after the frog had remained motionless for ~ 1 min. The other direction was selected and the same procedure was conducted again after a 2-min break. The rotation direction of the stimulus for the first five circles was randomized between blocks to offset possible bias. After the behavioral tests had been completed for each individual, the cup was washed and water was added for the next individual, and the subject was returned to its home tank.

Before EEG signal recordings, the subject was placed in the cup and connected to the signal acquisition system (OmniPlex 64-D, Plexon, USA) for habituating for ~ 10 min. The low-pass filter and

notch filter of the amplifiers and the sampling frequency were set at 100, 50 and 1000 Hz, respectively. The stimulus presentation was the same as for the behavioral tests. The experimenter pressed a button as soon as the anti-predatory behaviors of the subjects were elicited so that a trigger would be sent to the signal acquisition system and a red light-emitting diode outside the white opaque plastic cylinder would light for synchronizing behavioral and EEG data.

Data processing

Based on a previous study conducted in toads (Lippolis et al., 2002), we analyzed anti-predatory behaviors including avoiding responses (e.g. attack responses, backwards walks, and sideways or forward jumps), but not other behaviors, such as standing still and directing responses towards the stimulus (arching, lowering and exhaling), because of the difficulty in discriminating them. Anti-predatory behavioral responses in the visual midline (but not around the midline) were not considered or analyzed (Vallortigara et al., 1998). Accordingly, the numbers of ‘avoiding responses’ for each visual field and each rotation direction were counted. Furthermore, laterality preference for each subject was calculated using a laterality index (LI) (Bisazza et al., 2000), i.e. the ratio of the difference in numbers of anti-predatory responses between the RVF and LVF and the total number of these responses. Values significantly higher than 0 indicate a right-eye bias, whereas values significantly lower than 0 indicate a left-eye bias. In addition, we measured the avoiding angle for each subject towards the stimulus using a screen ruler software package (MB-Ruler 4.0, Markus Bader Software Solutions, Iffezheim, Germany). To test whether the subject responded uniformly when the stimulus was located in different positions of the animal’s visual fields measured previously (Shen et al., 2019), the numbers of responses and LI for each direction were acquired for the binocular visual field (from -14 to $+14$ deg), the middle part of the monocular visual field (from -14 to -60 or 14 to 60 deg) and the last part of the monocular visual field (from -60 to -150 or 60 to 150 deg).

Prior to analyzing power spectra, artifact-free 3 s EEG segments before the onset of every anti-predatory response were extracted. The EEG raw data were filtered offline using a band-pass filter of 0.5–45 Hz, downsampled at 512 Hz and divided into 1 s epochs. Using Welch’s method with 0.5 Hz resolution and Hamming window, EEG power spectra were calculated for each epoch, channel, visual condition (i.e. out of sight, LVF and RVF) and EEG band (i.e. delta, theta, alpha and beta) for every individual (Fang et al., 2012a). Power spectra were averaged across the three epochs before further statistical analysis.

Statistical analyses

The Shapiro–Wilk W test and Levene’s test were used to assess the normality of distribution and the homogeneity of variances of the values, respectively. Because the behavioral data failed to meet the statistical assumptions, the Wilcoxon signed ranks test was conducted for the eye preferences of the subjects during anti-predatory responses, while the Mann–Whitney U -test was used to test the differences in numbers of anti-predatory responses between males and females. In addition, the one-sample Wilcoxon signed ranks test was used to assess visual lateralization at group level. For electrophysiological data, there were nine frogs (five males and four females) that responded to the predator stimulus in both the LVF and RVF during anti-clockwise direction, of which four (two males and two females) responded to the predator stimulus in both the LVF and RVF during the clockwise direction. Two-way repeated-measures ANOVA was conducted with the factors of ‘brain area’ (LT, RT, LD, RD, LM and



Fig. 2. The testing apparatus for behavioral and EEG experiments on *N. daunchina*. The subject was placed in a cylindrical cup made of transparent polymethyl methacrylate (PMMA), which was hung in the middle of a U-shaped frame. A bar made of transparent PMMA was bent to form a right angle and adhered onto a PMMA board placed on the electric turntable. A white plastic wafer was adhered to the bottom of the cup to try to avoid visual interference. In addition, a white opaque plastic cylinder surrounded all the components.

RM) and ‘visual condition’ (out of sight, LVF and RVF) for EEG power spectra in the anti-clockwise direction. Both main effects and interactions were examined. If the interaction was significant, the simple effects analysis was applied. If ANOVA returned a significant difference, multiple comparisons were conducted using the least significant differences test. Greenhouse–Geisser epsilon values were employed when the assumption of sphericity was violated. Effect sizes for ANOVAs were estimated via partial η^2 (the values 0.20, 0.50 and 0.80 denote small, medium and large effect sizes, respectively) (Cohen, 1992). For the clockwise direction, the values failed to meet the statistical assumptions. Accordingly, Friedman test was conducted for the factors brain area and visual condition, but not considering sex because of small sample size. SPSS software (release 23.0) was employed for statistical analysis and $P < 0.05$ was considered significant.

RESULTS

The results of anti-predatory behaviors

For all subjects, regardless of sex, no significant eye preferences were found in the control condition for total (pooled data regardless of the rotation direction of the stimuli; $Z = -0.381$, $N = 29$, $P = 0.703$), clockwise ($Z = -0.504$, $N = 29$, $P = 0.614$) and anti-clockwise ($Z = -1.415$, $N = 29$, $P = 0.157$) directions (Fig. 3A). For females, there was no visual bias for total ($Z = -1.133$, $N = 15$, $P = 0.257$), clockwise ($Z = -0.642$, $N = 15$, $P = 0.521$) and anti-clockwise ($Z = -0.832$, $N = 15$, $P = 0.406$) directions (Fig. 3B). Similarly, for males, there was no visual bias for total ($Z = -0.611$, $N = 14$,

$P = 0.541$), clockwise ($Z = -1.399$, $N = 14$, $P = 0.180$) and anti-clockwise ($Z = -1.311$, $N = 14$, $P = 0.190$) directions (Fig. 3C). For all subjects, no significant difference between LI and 0 was found for the pooled data regardless of the visual field and rotation direction (VFA; $P = 0.753$), the pooled data for the clockwise direction regardless of the visual field (CVFA; $P = 0.975$) and the pooled data for the anti-clockwise direction regardless of the visual field (AVFA; $P = 0.496$; Fig. 3D). In addition, there was no significant difference between the two sexes for total, clockwise and anti-clockwise directions.

When the model snake head was presented, all subjects had a tendency to left-eye preference for total, anti-clockwise and clockwise directions, although this difference did not reach statistical significance (Fig. 3E and Fig. 4). However, significant left-eye preference was shown for the last part of the monocular visual field (from -60 to -150 or 60 to 150 deg) under anti-clockwise ($Z = -2.326$, $N = 47$, $P = 0.020$; $P = 0.035$ for LI) but not clockwise ($Z = -0.212$, $N = 47$, $P = 0.832$; $P = 0.935$ for LI) directions. No eye bias could be found for the binocular visual field (from -14 to $+14$ deg; for clockwise, $Z = -1.155$, $N = 13$, $P = 0.248$ and $P = 0.317$ for LI; for anti-clockwise, $Z = -1.414$, $N = 13$, $P = 0.157$ and $P = 0.180$ for LI) and the middle part of the monocular visual field (from -14 to -60 or 14 to 60 deg; for clockwise, $Z = -0.890$, $N = 35$, $P = 0.374$ and $P = 0.452$ for LI; for anti-clockwise, $Z = -0.383$, $N = 35$, $P = 0.701$ and $P = 0.802$ for LI; Fig. 4). For females, significant left-eye preference was shown for total ($Z = -2.271$, $N = 20$, $P = 0.023$), but not for anti-clockwise ($Z = -1.733$, $N = 20$, $P = 0.083$) and clockwise

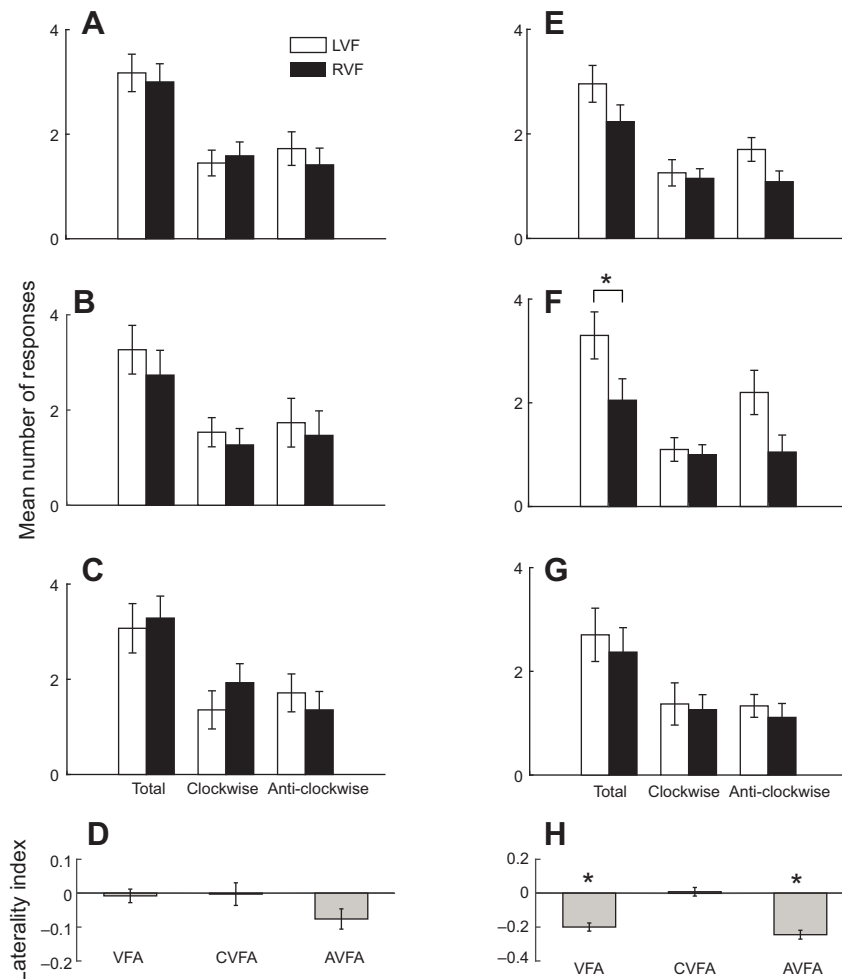


Fig. 3. Numbers of anti-predatory responses for total, clockwise and anti-clockwise directions in *N. daunchina*.

(A–C, E–G) Mean numbers of responses when the control (leaf) was presented for the two sexes (A), females (B) and males (C), and when the predator stimulus (the head of the snake model) was presented for the two sexes (E), females (F) and males (G). (D, H) Laterality index (LI) for the control (D) and the predator stimulus (H). ‘Total’ indicates pooled data regardless of the rotation direction of the stimuli; ‘clockwise’ and ‘anti-clockwise’ indicate the rotation direction of the stimuli; ‘VFA’ indicates the pooled data regardless of visual field and rotation direction; ‘CVFA’ indicates the pooled data during the clockwise direction regardless of the visual field; ‘AVFA’ indicates the pooled data during the anti-clockwise direction regardless of the visual field. * $P < 0.05$ (one-sample Wilcoxon signed rank test for D and H; Wilcoxon signed ranks test for the others). Data are means \pm s.e.m.

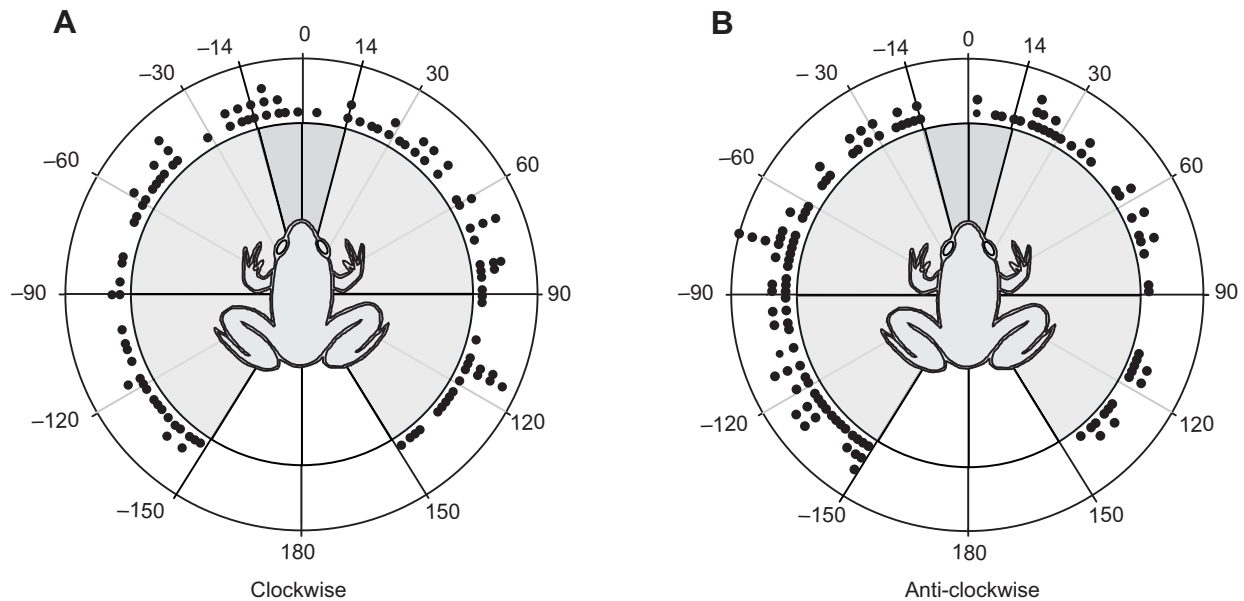


Fig. 4. Anti-predatory responses in *N. daunchina* with respect to visual fields. (A,B) Anti-predatory responses when the predator stimulus was circled clockwise (A) and anti-clockwise (B). The positions of anti-predatory responses are denoted by the angles (in deg) of predator stimuli from the frog's midline when the stimuli evoked the frog's anti-predatory response. The darker-shaded regions denote the binocular visual fields, the lighter-shaded regions denote the monocular visual fields, and the white regions denote out of sight visual fields. Note that the very few responses when the predator stimulus was out of sight are not shown. The extent of visual fields in the horizontal plane at eye level was determined by measuring the angle at which the pupil could no longer be seen using an ophthalmoscope (Lippolis et al., 2002; Martin, 1984; Shen et al., 2019).

($Z=-0.476$, $N=20$, $P=0.634$; Fig. 3F). By contrast, for males, no significant visual bias was found for total ($Z=-0.610$, $N=27$, $P=0.542$), clockwise ($Z=-0.154$, $N=27$, $P=0.877$) and anti-clockwise ($Z=-0.446$, $N=27$, $P=0.656$; Fig. 3G). Similar sex differences could be found for the last part of the monocular visual field but not for other parts. Furthermore, for all subjects, the LI was significantly smaller than 0 for VFA ($P=0.044$) and AVFA ($P=0.026$), but not CVFA ($P=0.934$; Fig. 3H). In addition, there was no significant difference in LI between the two sexes for total, clockwise and anti-clockwise.

Power spectra for each EEG band during anti-predatory behaviors

For delta band and clockwise direction, the main effects of the factor brain area, but not visual condition, were significant for out of sight ($\chi^2=12.571$, d.f.=5, $P=0.028$) and LVF ($\chi^2=13.571$, d.f.=5, $P=0.019$; Fig. 5A). However, there were no significant differences between the left and right sides of the telencephalon, diencephalon or mesencephalon (LT, RT, LD, RD, LM and RM, respectively) for each visual condition. For the anti-clockwise direction, the main effects were significant for the factors brain area ($F_{5,40}=11.842$; $P<0.001$, partial $\eta^2=0.597$) and visual condition ($F_{2,16}=3.666$; $P=0.049$, partial $\eta^2=0.314$). There were no significant differences between the left and right hemispheres for each visual condition; however, the delta power spectra for LVF were significantly higher than those for out of sight ($P<0.05$; Fig. 5B).

For theta band and clockwise direction, the main effects of the factor brain area, but not visual condition, were significant for LVF ($\chi^2=15.000$, d.f.=5, $P=0.010$) and RVF ($\chi^2=11.429$, d.f.=5, $P=0.044$; Fig. 5C), while for the anti-clockwise direction, the main effect was significant for the factor brain area ($F_{5,40}=16.785$; $P<0.001$, partial $\eta^2=0.677$; Fig. 5D). However, there were no significant differences between the left and right hemispheres for each visual condition in both directions.

For alpha band and clockwise direction, the main effects of the factor brain area were significant for out of sight ($\chi^2=14.286$, d.f.=5, $P=0.014$) and LVF ($\chi^2=16.714$, d.f.=5, $P=0.005$), while the main effect of the factor visual condition was significant for LM ($\chi^2=6.500$, d.f.=2, $P=0.039$). However, there were no significant differences between the left and right hemispheres for each visual condition or between different visual conditions for LM (Fig. 5E). For the anti-clockwise direction, the main effect was significant for the factor brain area ($F_{5,40}=17.515$; $P<0.001$, partial $\eta^2=0.686$), and the interaction between brain area and visual condition was also significant ($F_{10,80}=4.247$; $P<0.001$, partial $\eta^2=0.347$). The power spectra of the LD were significantly higher than those of the RD for out of sight ($P<0.05$), and the power spectra of the RT for LVF were significantly higher than those for out of sight ($P<0.05$; Fig. 5F).

For beta band and clockwise direction, the main effects of the factor brain area were significant for out of sight ($\chi^2=12.286$, d.f.=5, $P=0.031$) and LVF ($\chi^2=16.143$, d.f.=5, $P=0.006$), while the main effect of the factor visual condition was significant for LM ($\chi^2=6.500$, d.f.=2, $P=0.039$). However, there were no significant differences between the left and right hemispheres for each visual condition or between different visual conditions for LM (Fig. 5G). For the anti-clockwise direction, the main effect was significant for the factor brain area ($F_{5,40}=6.082$; $P<0.001$, partial $\eta^2=0.432$; Fig. 5H). However, there were no significant differences between the left and right hemispheres for each visual condition.

DISCUSSION

Our results showed no significant differences in the numbers of anti-predatory responses for the control (leaf); however, the number of anti-predatory responses for the LVF was significantly greater than that for the RVF when the predator stimulus was presented, although for males this difference did not reach statistical significance. Compared with no stimulus in the visual field, the power spectra of delta band were significantly greater when the predator stimulus was

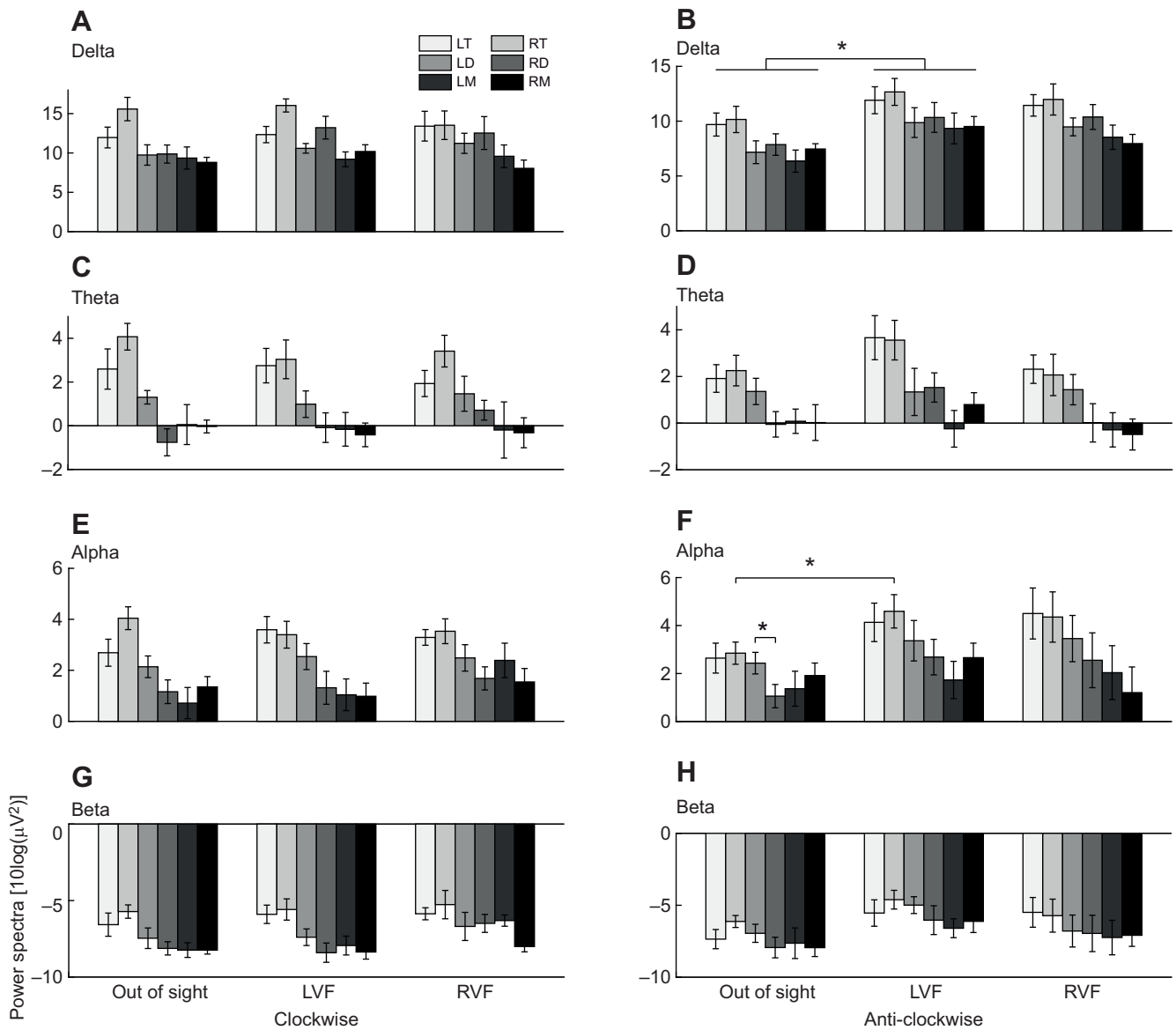


Fig. 5. EEG power spectra for each brain region and visual condition in *N. daunchina*. (A–H) Delta (A,B), theta (C,D), alpha (E,F) and beta (G,H) EEG bands for the clockwise (A,C,E,G) and anti-clockwise (B,D,F,H) directions. LD, left diencephalon; LM, left mesencephalon; LT, left telencephalon; LVF, left visual field; RD, right diencephalon; RM, right mesencephalon; RT, right telencephalon; RVF, right visual field. * $P < 0.05$ (two-way repeated-measures ANOVA for anti-clockwise direction, Friedman test for clockwise direction). Data are means \pm s.e.m.

moved into the LVF in an anti-clockwise direction. Generally, the power spectra of each band for the LVF were higher in the right hemisphere than in the left hemisphere. These results support a left-eye advantage for mediating monitoring of a predator in music frogs, and that low-frequency EEG oscillations possibly underlie this left-eye/right-hemisphere advantage.

Left-eye preference for vigilance responses to the predator

Animals are continuously gathering information through their visual field to make the optimal cognitive decisions for survival and reproduction success, during which predatory and anti-predatory behaviors are crucial for survival, and survival hinges on the early detection of predators (Fernández-Juricic, 2012). Here, we found no lateralized eye use when leaves of simple structure were presented, consistent with the idea that visual processing of a simple stimulus is not functionally lateralized and is carried out in the left and right optic tectum at a lower processing level of neural circuits with an

equivalent role (Rogers, 2002b; Vallortigara, 2000). Similarly, compared with a complex prey stimulus, a simple stimulus evoked non-significant eye lateralization for predatory responses in toads (Robins and Rogers, 2004) and music frogs (Shen et al., 2019), suggesting that a simple structure lacking appendages does not elicit lateralized prey behavior, unlike a complex prey stimulus.

When the model snake head appeared in the LVF it elicited more anti-predatory responses than when moved into the RVF, indicating that left-eye advantage exists during anti-predatory behavior in the music frog. In line with this, previous studies have found that more escape and defensive responses were evoked when the model snake was in the left monocular visual field in toads and marsupial mice (Lippolis et al., 2002, 2005). Because the lateral field of each eye projects mainly to the contralateral side of the brain in most species of vertebrates (Vallortigara et al., 1999), these findings, including the present results, suggest that the neural structures located in the right hemisphere are more specialized for anti-predatory behavior compared

with those located in the left hemisphere. The right hemisphere might therefore be more involved in response to unexpected, dangerous events or negative stimuli, and the model snake head represents a negative stimulus for the subject. Our results support both the ‘valence theory’, which presumes that the right hemisphere is mainly used to process negative stimuli (Prete et al., 2015; Siniscalchi et al., 2013), and the ‘brain’s right hemisphere’ theory, which proposes that the right brain is preferentially used to process information concerning novel events in which the animal may be in an intense emotional state (e.g. aggression, fear and escape behavior) and should respond rapidly (MacNeilage et al., 2009; Rogers et al., 2013).

Left-eye/right-hemisphere dominance to control aggressive and anti-predatory behaviors, exposing the left side of the body to a predator or conspecifics, might be advantageous during novel or urgent situations to execute physical behaviors for protection and escape (Quaresmini et al., 2014). Consistent with this, right hemispheric superiority underlies the perceptual lateralization in social behaviors of many phylogenetically diverse taxa (Brancucci et al., 2009; Salva et al., 2012). For example, highly aggressive or anti-predatory behaviors are significantly more likely to occur when the left eye sees an opponent or predator, which is found in a variety of species including cuttlefish (Schnell et al., 2016; Schnell et al., 2019), locusts (Romano et al., 2017), amphibians (Robins and Rogers, 2006), reptiles (Hews et al., 2004), birds (Vallortigara et al., 2001), mammals (Austin and Rogers, 2012, 2014), primates (Casperd and Dunbar, 1996; Quaresmini et al., 2014) and even humans (Forrester et al., 2014). These findings suggest that the brain asymmetry could be inherited from a common ancestor (Rogers and Andrew, 2002). Social pressures and evolutionarily stable strategies can have an influence on visual lateralization. The former produce fitness advantages for individuals that have their biases aligned with other individuals in a group (Ghirlanda and Vallortigara, 2004), while the latter are based exclusively on fitness consequences that exist during intraspecific competition and coordination (Ghirlanda et al., 2009). Furthermore, visual lateralization for predator and prey can be affected by other factors, including the complexity of stimulus structure and familiarity of stimuli (Ewert and Kehl, 1978; Ingle and Mckinley, 1978), the sex and age of subjects (Thieltges et al., 2011), and the attributes of the microhabitat (Fernández-Juricic, 2012; Shepard, 2007). Interestingly, our results showed that significant lateralized defensive responses were exhibited only for the last part of the monocular visual field (comparing the numbers of responses from -60 to -150 deg with those from 60 and 150 deg) for the anti-clockwise direction, suggesting that more defensive responses could be evoked when the predator stimulus was about to disappear anti-clockwise. Similar findings show that primates are more likely to direct agonistic responses towards a conspecific in their extreme LVF than to one in their RVF, indicating dominance of the right hemisphere in the processing of emotional information (Casperd and Dunbar, 1996).

Our results also showed significant left-eye advantage in females, but not males, when the predator stimulus moved into the LVF. Moreover, the number of behavioral responses in females was greater than that in males, although this difference did not reach statistical significance. These results suggest that there could be sex differences in laterality, consistent with a previous study that showed differences in strength and direction of laterality between male and female pigs (Camerlink et al., 2018). The sex differences imply that, at least to some extent, females are more careful, cautious and fearful of environmental stimuli (especially dangerous ones such as predators) than males, which has been suggested to be related to the influence of corticosterone (in birds), estrogen and testosterone (Rogers et al., 2013).

Low-frequency EEG oscillations might govern left-eye advantage during anti-predatory behaviors

In this study, the power spectra of delta band for the LVF were significantly greater than those for no stimulus in the visual field when the predator stimulus was moved into the LVF anti-clockwise, but not clockwise. In line with this, defensive behaviors in toad (*Bufo regularis*) and common frog (*Rana temporaria*) are accompanied by an extensive increase in delta band (Laming, 1982). Delta oscillations are continuously predominant EEG rhythms in poikilotherms, and the highest amplitude exists during active waking but not during sleep (Knyazev, 2012). Furthermore, the delta oscillations show an arousal reaction, which consists of growth in delta amplitude and synchrony, unlike those in birds and mammals, which show quite different arousal reactions of low amplitude and mixed frequencies (Rial et al., 2007). They play a key role in the brainstem system, as they exert regulatory effects on the cardiovascular, respiratory and motor systems, processing of the afferences and vigilance (Langhorst et al., 1992). For example, enhancements in delta band can be triggered by biological dangers and rewards, which are involved in attention, saliency detection and decision making (Başar-Eroglu et al., 1992; Knyazev, 2012). Thus, it is reasonable to speculate that the increase in delta power spectra might result from demands for maintaining high vigilance and saliency detection during anti-predatory behaviors.

Recent studies suggest that alpha oscillations are related to attention and may serve as an attentional mechanism for focusing on relevant stimuli, either through increasing signal-to-noise ratios within the cortex or via inhibition of conflicting and/or unnecessary processes for the task in hand (Klimesch, 2012). For example, previous studies have shown that processing inputs and suppressing information is mainly associated with an increase in alpha power (Händel et al., 2011; Jensen et al., 2012). Moreover, the processing of the stimuli needed to make corresponding behavioral responses might be a synchronization process related to alpha oscillations. Anti-predatory responses are the decision outcome of the sensorimotor network in the brain, and we here found that increases in power output within the alpha band in the RT matched closely with the dynamic properties of the visual signals moved into the LVF anti-clockwise. Because important neuroanatomical features of vertebrate brain have been conserved during evolution (Finlay et al., 2001; Northcutt, 2002), alpha oscillations in anurans would be expected to increase while making a decision, such as in prey and anti-predatory responses, which require time for collecting and processing input information, such as when the predator appears in the LVF of animals. This speculation is consistent with a previous study that showed that defensive behaviors in anurans result in an increase in alpha oscillations (Hobson, 1967). Moreover, right hemisphere dominance exists during stimulus-driven shifts in spatial attention and target detection (Shulman et al., 2010), which might have evolved in amphibians and has been retained insofar as the RT of frogs is engaged in spatial attention and target detection for anti-predation.

Although no significant differences were found between the two sides of the brain areas, the power spectra of theta and beta bands were greater when the predator stimulus was moved into the LVF anti-clockwise than for other visual conditions. Distributed oscillatory systems with various bands act as resonant communication networks through large populations of neurons; these oscillations might be vital for functional communication in the brain in relation to vigilance, defensive, memory and integrative functions (Başar et al., 2001). Thus, their power increase in the right hemisphere might play a crucial role in anti-predatory behavior (i.e. vigilant and defensive

state). EEG power spectra increases in output within each EEG band, especially in delta band, matched closely with the dynamic properties of the visual signals moved into the LVF anti-clockwise, but not clockwise, which might reflect the fact that anti-predatory responses require time for the collection and processing of input information, similar to predatory responses (Shen et al., 2019). In summary, music frogs exhibited a visual lateralization for anti-predatory behavior with the left eye, which was in accord with results from previous studies on other species, and preferred to process anti-predatory cues with the right brain hemisphere. The power EEG band, especially in delta and alpha, increases in the right hemisphere possibly underlie this left-eye advantage for anti-predatory behavior. Further study is required to verify the specific functions of each frequency band in lateralization of anti-predatory behavior in music frogs.

Acknowledgements

The authors gratefully acknowledge Xiaoqian Sun and Yue Yang for assistance with fieldwork, and all members of the Behavioral Neuroscience Group for discussions and help with the experiments reported.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: G.F.; Methodology: J. Shen, K.F., G.F.; Software: G.F.; Formal analysis: J. Shen; Investigation: K.F., P.L., Y.F., J.Y., D.S., J. Song; Writing - original draft: J. Shen; Writing - review & editing: G.F.; Supervision: G.F.; Project administration: G.F.; Funding acquisition: G.F.

Funding

This work was supported by grants from the National Natural Science Foundation of China (31970422 and 31672305) and the Foundation of Key Laboratory of Southwest China Wildlife Resources Conservation (Ministry of Education), China West Normal University (HNYB19-02).

References

- Austin, N. P. and Rogers, L. J. (2012). Limb preferences and lateralization of aggression, reactivity and vigilance in feral horses, *Equus caballus*. *Anim. Behav.* **83**, 239–247. doi:10.1016/j.anbehav.2011.10.033
- Austin, N. P. and Rogers, L. J. (2014). Lateralization of agonistic and vigilance responses in Przewalski horses (*Equus przewalskii*). *Appl. Anim. Behav. Sci.* **151**, 43–50. doi:10.1016/j.applanim.2013.11.011
- Başar, E., Başar-Eroglu, C., Karakaş, S. and Schürmann, M. (2001). Gamma, alpha, delta, and theta oscillations govern cognitive processes. *Int. J. Psychophysiol.* **39**, 241–248. doi:10.1016/S0167-8760(00)00145-8
- Başar-Eroglu, C., Başar, E., Demiralp, T. and Schürmann, M. (1992). P300-response: possible psychophysiological correlates in delta and theta frequency channels. A review. *Int. J. Psychophysiol.* **13**, 161–179. doi:10.1016/0167-8760(92)90055-G
- Bisazza, A., Cantalupo, C., Capocchiano, M. and Vallortigara, G. (2000). Population lateralisation and social behaviour: a study with 16 species of fish. *Lateralality* **5**, 269–284. doi:10.1080/713754381
- Brancucci, A., Lucci, G., Mazzatenta, A. and Tommasi, L. (2009). Asymmetries of the human social brain in the visual, auditory and chemical modalities. *Philos. Trans. R. Soc. B* **364**, 895–914. doi:10.1098/rstb.2008.0279
- Camerlink, I., Menneson, S., Turner, S. P., Farish, M. and Arnott, G. (2018). Lateralization influences contest behaviour in domestic pigs. *Sci. Rep.* **8**, 12116. doi:10.1038/s41598-018-30634-z
- Casperd, J. M. and Dunbar, R. I. M. (1996). Asymmetries in the visual processing of emotional cues during agonistic interactions by gelada baboons. *Behav. Process.* **37**, 57–65. doi:10.1016/0376-6357(95)00075-5
- Chang, M. L. Y. and Hsü, H. F. (1933). Study of some amphibians from Szechuan: Contributions from the Biological Laboratory of the Science Society of China. *Zoological Series* **8**, 137–181.
- Cohen, J. (1992). A power primer. *Psychol. Bull.* **112**, 155–159. doi:10.1037/0033-2909.112.1.155
- Concha, M. L., Bianco, I. H. and Wilson, S. W. (2012). Encoding asymmetry within neural circuits. *Nat. Rev. Neurosci.* **13**, 832–843. doi:10.1038/nrn3371
- Cronin, T. W. (2005). The visual ecology of predator–prey interactions. In *Ecology of Predator–Prey Interactions* (ed. P. Barbosa and I. Castellanos), pp. 105–138. Oxford: Oxford University Press.
- Dadda, M., Sovrano, V. A. and Bisazza, A. (2003). Temporal pattern of social aggregation in tadpoles and its influence on the measurement of lateralised response to social stimuli. *Physiol. Behav.* **78**, 337–341. doi:10.1016/S0031-9384(02)01001-6
- Ewert, J.-P. and Kehl, W. (1978). Configurational prey-selection by individual experience in the toad *Bufo bufo*. *J. Comp. Physiol. A Sens. Neural. Behav. Physiol.* **126**, 105–114. doi:10.1007/BF00666362
- Fan, Y. Z., Yue, X. Z., Yang, J., Shen, J. Y., Shen, D., Tang, Y. Z. and Fang, G. Z. (2019). Preference of spectral features in auditory processing for advertisement calls in the music frogs. *Front. Zool.* **16**, 13. doi:10.1186/s12983-019-0314-0
- Fang, G. Z., Chen, Q., Cui, J. G. and Tang, Y. Z. (2012a). Electroencephalogram bands modulated by vigilance states in an anuran species: a factor analytic approach. *J. Comp. Physiol. A Sens. Neural. Behav. Physiol.* **198**, 119–127. doi:10.1007/s00359-011-0693-y
- Fang, G. Z., Yang, P., Cui, J. G., Yao, D. Z., Brauth, S. E. and Tang, Y. Z. (2012b). Mating signals indicating sexual receptiveness induce unique spatio-temporal EEG theta patterns in an anuran species. *PLoS ONE* **7**, e52364. doi:10.1371/journal.pone.0052364
- Fang, G. Z., Yang, P., Xue, F., Cui, J. G., Brauth, S. E. and Tang, Y. Z. (2015). Sound classification and call discrimination are decoded in order as revealed by event-related potential components in frogs. *Brain. Behav. Evol.* **86**, 232–245. doi:10.1159/000441215
- Fernández-Juricic, E. (2012). Sensory basis of vigilance behavior in birds: synthesis and future prospects. *Behav. Process.* **89**, 143–152. doi:10.1016/j.beproc.2011.10.006
- Ferrari, M. C. O., McCormick, M. I., Mitchell, M. D., Allan, B. J. M., Gonçalves, E. J. and Chivers, D. P. (2017). Daily variation in behavioural lateralization is linked to predation stress in a coral reef fish. *Anim. Behav.* **133**, 189–193. doi:10.1016/j.anbehav.2017.09.020
- Finlay, B. L., Darlington, R. B. and Nicastro, N. (2001). Developmental structure in brain evolution. *Behav. Brain. Sci.* **24**, 263–278. doi:10.1017/S0140525X01003958
- Fite, K. V. and Scalia, F. (1976). Central visual pathways in the frog. In *The Amphibian Visual System A Multidisciplinary Approach* (ed. K. V. Fite), pp. 87–118. New York: A Subsidiary of Harcourt Brace Jovanovich Press.
- Forrester, G. S., Crawley, M. and Palmer, C. (2014). Social environment elicits lateralized navigational paths in two populations of typically developing children. *Brain. Cogn.* **91**, 21–27. doi:10.1016/j.bandc.2014.07.005
- Franklin, W. E. and Lima, S. L. (2001). Laterality in avian vigilance: do sparrows have a favourite eye? *Anim. Behav.* **62**, 879–885. doi:10.1006/anbe.2001.1826
- Frasnelli, E. (2013). Brain and behavioral lateralization in invertebrates. *Front. Psychol.* **4**, 939. doi:10.3389/fpsyg.2013.00939
- Frasnelli, E., Vallortigara, G. and Rogers, L. J. (2012). Left–right asymmetries of behaviour and nervous system in invertebrates. *Neurosci. Biobehav. Rev.* **36**, 1273–1291. doi:10.1016/j.neubiorev.2012.02.006
- Ghirlanda, S. and Vallortigara, G. (2004). The evolution of brain lateralization: a game-theoretical analysis of population structure. *Proc. Biol. Sci.* **271**, 853–857. doi:10.1098/rspb.2003.2669
- Ghirlanda, S., Frasnelli, E. and Vallortigara, G. (2009). Intraspecific competition and coordination in the evolution of lateralization. *Philos. Trans. R. Soc. B* **364**, 861–866. doi:10.1098/rstb.2008.0227
- Halpern, M., Scalia, F. and Riss, W. (1968). On the nature of the hippocampal commissure in the frog. *Brain. Behav. Evol.* **1**, 155–174. doi:10.1159/000125501
- Händel, B. F., Haarmeier, T. and Jensen, O. (2011). Alpha oscillations correlate with the successful inhibition of unattended stimuli. *J. Cognitive. Neurosci.* **23**, 2494–2502. doi:10.1162/jocn.2010.21557
- Hellige, J. B. (1993). *Hemispheric Asymmetry: What's Right and What's Left*. Cambridge, MA: Harvard University Press.
- Hemmi, J. M. and Zeil, J. (2005). Animals as prey: perceptual limitations and behavioural options. *Mar. Ecol. Prog. Ser.* **287**, 274–278.
- Hews, D. K. and Worthington, R. A. (2001). Fighting from the right side of the brain: left visual field preference during aggression in free-ranging male tree lizards (*Urosaurus ornatus*). *Brain Behav. Evol.* **58**, 356–361. doi:10.1159/000057576
- Hews, D. K., Castellano, M. and Hara, E. (2004). Aggression in females is also lateralized: left-eye bias during aggressive courtship rejection in lizards. *Anim. Behav.* **68**, 1201–1207. doi:10.1016/j.anbehav.2003.11.024
- Hobson, J. A. (1967). Respiration and EEG synchronization in the frog. *Nature* **213**, 988–989. doi:10.1038/213988a0
- Ingle, D. and McKinley, D. (1978). Effects of stimulus configuration on elicited prey catching by the marine toad (*Bufo marinus*). *Anim. Behav.* **26**, 885–891. doi:10.1016/0003-3472(78)90154-9
- Jensen, O., Bonnefond, M. and VanRullen, R. (2012). An oscillatory mechanism for prioritizing salient unattended stimuli. *Trends. Cogn. Sci.* **16**, 200–206. doi:10.1016/j.tics.2012.03.002
- Kandel, E. R., Schwartz, J. H., Jessell, T. M., Siegelbaum, S. A. and Hudspeth, A. J. (2013). *Principles of Neural Science*. New York: McGraw-Hill Press.
- Klimesch, W. (2012). Alpha-band oscillations, attention, and controlled access to stored information. *Trends. Cogn. Sci.* **16**, 606–617. doi:10.1016/j.tics.2012.10.007
- Knyazev, G. G. (2012). EEG delta oscillations as a correlate of basic homeostatic and motivational processes. *Neurosci. Biobehav. Rev.* **36**, 677–695. doi:10.1016/j.neubiorev.2011.10.002

- Laming, P. R. (1982). Electroencephalographic correlates of behavior in the anurans *Bufo regularis* and *Rana temporaria*. *Behav. Neural Biol.* **34**, 296-306. doi:10.1016/S0163-1047(82)91678-8
- Langhorst, P., Lambert, M., Kluge, W. and Rittweger, J. (1992). Different modes of dampening influence from baroreceptors are determined by the functional organization of the NTS neuronal network. *J. Auton. Nerv. Syst.* **41**, 141-156. doi:10.1016/0165-1838(92)90136-5
- Lima, S. L. and Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* **68**, 619-640. doi:10.1139/z90-092
- Lippolis, G., Bisazza, A., Rogers, L. J. and Vallortigara, G. (2002). Lateralisation of predator avoidance responses in three species of toads. *Laterality* **7**, 163-183. doi:10.1080/13576500143000221
- Lippolis, G., Westman, W., McAllan, B. and Rogers, L. (2005). Lateralization of escape responses in the striped-faced dunnart, *Sminthopsis macroura* (Dasyuridae: Marsupialia). *Laterality* **10**, 457-470. doi:10.1080/13576500442000210
- MacNeilage, P. F., Rogers, L. J. and Vallortigara, G. (2009). Origins of the left and right brain. *Sci. Am.* **301**, 60-67. doi:10.1038/scientificamerican0709-60
- Martin, G. R. (1984). The visual fields of the tawny owl. *Strix aluco* L. *Vision Res.* **24**, 1739-1751. doi:10.1016/0042-6989(84)90005-1
- Mazza, V. and Pagano, S. (2017). Electroencephalographic asymmetries in human cognition. In *Lateralized Brain Functions: Methods in Human and Non-Human Species* (ed. L. J. Rogers and G. Vallortigara), pp. 407-439. New York: Springer Nature.
- Northcutt, R. G. (2002). Understanding Vertebrate Brain Evolution. *Integr. Comp. Biol.* **42**, 743-756. doi:10.1093/icb/42.4.743
- Pellitteri-Rosa, D. and Gazzola, A. (2018). Context-dependent behavioural lateralization in the European pond turtle, *Emys orbicularis* (Testudines, Emydidae). *J. Exp. Biol.* **221**, 1-8. doi:10.1242/jeb.186775
- Prete, G., Laeng, B., Fabri, M., Foschi, N. and Tommasi, L. (2015). Right hemisphere or valence hypothesis, or both? The processing of hybrid faces in the intact and callosotomized brain. *Neuropsychologia* **68**, 94-106. doi:10.1016/j.neuropsychologia.2015.01.002
- Quaresmini, C., Forrester, G. S., Spiezio, C. and Vallortigara, G. (2014). Social environment elicits lateralized behaviors in gorillas (*Gorilla gorilla gorilla*) and chimpanzees (*Pan troglodytes*). *J. Comp. Psychol.* **128**, 276-284. doi:10.1037/a0036355
- Rial, R. V., Nicolau, M. C., Gamundi, A., Akaärir, M., Garau, C., Aparicio, S., Tejada, S., Moranta, D., Gené, L. and Esteban, S. (2007). Comments on evolution of sleep and the pallioplial connectivity in mammals and birds. *Brain Res. Bull.* **72**, 183-186. doi:10.1016/j.brainresbull.2007.01.003
- Robins, A. and Rogers, L. J. (2004). Lateralized prey-catching responses in the cane toad, *Bufo marinus*: analysis of complex visual stimuli. *Anim. Behav.* **68**, 767-775. doi:10.1016/j.anbehav.2003.12.014
- Robins, A. and Rogers, L. J. (2006). Lateralized visual and motor responses in the green tree frog, *Litoria caerulea*. *Anim. Behav.* **72**, 843-852. doi:10.1016/j.anbehav.2006.01.022
- Rogers, L. J. (2000). Evolution of hemispheric specialization: advantages and disadvantages. *Brain Lang.* **73**, 236-253. doi:10.1006/brln.2000.2305
- Rogers, L. J. (2002a). Lateralised brain function in anurans: comparison to lateralisation in other vertebrates. *Laterality* **7**, 219-239. doi:10.1080/13576500244000012
- Rogers, L. J. (2002b). Lateralization in vertebrates: Its early evolution, general pattern, and development. *Adv. Study. Behav.* **31**, 107-161. doi:10.1016/S0065-3454(02)80007-9
- Rogers, L. J. and Andrew, R. J. (2002). *Comparative vertebrate lateralization*. Cambridge: Cambridge University Press.
- Rogers, L. J., Zucca, P. and Vallortigara, G. (2004). Advantages of having a lateralized brain. *Proc. Biol. Sci.* **271** Suppl. 6, S420-S422. doi:10.1098/rsbl.2004.0200
- Rogers, L. J., Vallortigara, G. and Andrew, R. J. (2013). *Divided Brains: The Biology and Behaviour of Brain Asymmetries*. Cambridge: Cambridge University Press.
- Romano, D., Benelli, G. and Stefanini, C. (2017). Escape and surveillance asymmetries in locusts exposed to a Guinea fowl-mimicking robot predator. *Sci. Rep.* **7**, 12825. doi:10.1038/s41598-017-12941-z
- Salva, O. R., Regolin, L., Mascalonzi, E. and Vallortigara, G. (2012). Cerebral and behavioural asymmetries in animal social recognition. *Comp. Cognit. Behav. Rev.* **7**, 110-138. doi:10.3819/ccbr.2012.70006
- Scalia, F. (1976). The optic pathway of the frog: nuclear organization and connections. In *Frog Neurobiology A Handbook* (ed. R. Llinás and W. Precht), pp. 385-404. Berlin: Springer Press.
- Schnell, A. K., Hanlon, R. T., Benkada, A. and Jozet-Alves, C. (2016). Lateralization of eye use in cuttlefish: opposite direction for anti-predatory and predatory behaviors. *Front. Physiol.* **7**, 620. doi:10.3389/fphys.2016.00620
- Schnell, A. K., Bellanger, C., Vallortigara, G. and Jozet-Alves, C. (2018). Visual asymmetries in cuttlefish during brightness matching for camouflage. *Curr. Biol.* **28**, R925-R926. doi:10.1016/j.cub.2018.07.019
- Schnell, A. K., Jozet-Alves, C., Hall, K. C., Radday, L. and Hanlon, R. T. (2019). Fighting and mating success in giant Australian cuttlefish is influenced by behavioural lateralization. *Proc. Biol. Sci.* **286**, 20182507. doi:10.1098/rspb.2018.2507
- Shen, J. Y., Fang, K., Fan, Y. Z., Song, J. J., Yang, J., Shen, D., Liu, Y. S. and Fang, G. Z. (2019). Dynamics of electroencephalogram oscillations underlie right-eye preferences in predatory behavior of the music frog. *J. Exp. Biol.* **222**, jeb212175. doi:10.1242/jeb.212175
- Shepard, D. B. (2007). Habitat but not body shape affects predator attack frequency on lizard models in the Brazilian Cerrado. *Herpetologica* **63**, 193-202. doi:10.1655/0018-0831(2007)63[193:HBNBSA]2.0.CO;2
- Shulman, G. L., Pope, D. L. W., Astafiev, S. V., McAvoy, M. P., Snyder, A. Z. and Corbetta, M. (2010). Right hemisphere dominance during spatial selective attention and target detection occurs outside the dorsal frontoparietal network. *J. Neurosci.* **30**, 3640-3651. doi:10.1523/JNEUROSCI.4085-09.2010
- Siniscalchi, M., Lusito, R., Vallortigara, G. and Quaranta, A. (2013). Seeing left- or right-asymmetric tail wagging produces different emotional responses in dogs. *Curr. Biol.* **23**, 2279-2282. doi:10.1016/j.cub.2013.09.027
- Thieltges, H., Lemasson, A., Kuczaj, S., Böye, M. and Blois-Heulin, C. (2011). Visual laterality in dolphins when looking at (un)familiar humans. *Anim. Cogn.* **14**, 303-308. doi:10.1007/s10071-010-0354-5
- Vallortigara, G. (2000). Comparative neuropsychology of the dual brain: a stroll through animals' left and right perceptual worlds. *Brain Lang.* **73**, 189-219. doi:10.1006/brln.2000.2303
- Vallortigara, G. (2006). The evolutionary psychology of left and right: costs and benefits of lateralization. *Dev. Psychobiol.* **48**, 418-427. doi:10.1002/dev.20166
- Vallortigara, G. and Rogers, L. J. (2005). Survival with an asymmetrical brain: advantages and disadvantages of cerebral lateralization. *Behav. Brain Sci.* **28**, 575-589. doi:10.1017/S0140525X05000105
- Vallortigara, G. and Rogers, L. J. (2020). A function for the bicameral mind. *Cortex* **124**, 274-285. doi:10.1016/j.cortex.2019.11.018
- Vallortigara, G., Rogers, L. J., Bisazza, A., Lippolis, G. and Robins, A. (1998). Complementary right and left hemifield use for predatory and agonistic behaviour in toads. *Neuroreport* **9**, 3341-3344. doi:10.1097/00001756-199810050-00035
- Vallortigara, G., Rogers, L. J. and Bisazza, A. (1999). Possible evolutionary origins of cognitive brain lateralization. *Brain Res. Rev.* **30**, 164-175. doi:10.1016/S0165-0173(99)00012-0
- Vallortigara, G., Cozzutti, C., Tommasi, L. and Rogers, L. J. (2001). How birds use their eyes: Opposite left-right specialization for the lateral and frontal visual hemifield in the domestic chick. *Curr. Biol.* **11**, 29-33. doi:10.1016/S0960-9822(00)00027-0
- Yue, X. Z., Fan, Y. Z., Xue, F., Brauth, S. E., Tang, Y. Z. and Fang, G. Z. (2017). The first call note plays a crucial role in frog vocal communication. *Sci. Rep.* **7**, 10128. doi:10.1038/s41598-017-09870-2