

RESEARCH ARTICLE

Dynamics of electroencephalogram oscillations underlie right-eye preferences in predatory behavior of the music frog

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ABSTRACT

Visual lateralization is a typical characteristic of many vertebrates; however, its underlying dynamic neural mechanism is unclear. In this study, predatory responses and dynamic brain activities were evaluated in the Emei music frog (*Nidirana daunchina*) to assess the potential eye preferences and their underlying dynamic neural mechanism, using behavioral and electrophysiological experiments, respectively. To do this, when the prey stimulus (live cricket and leaf as control) was moved around the frogs in both clockwise and anticlockwise directions at constant velocity, the number of predatory responses were counted and electroencephalogram (EEG) absolute power spectra for each band were measured for the telencephalon, diencephalon and mesencephalon. The results showed that: (1) no significant differences in the number of predatory responses could be found for the control (leaf), but the number of predatory responses for the right visual field (RVF) was significantly greater than that for the left visual field (LVF) when the live cricket was moved into the RVF clockwise; (2) compared with no stimulus in the visual field and stimulus in the LVF, the power spectra of each EEG band were greater when the prey stimulus was moved into the RVF clockwise; and (3) the power spectra of the theta, alpha and beta bands in the left diencephalon were significantly greater than those of the right counterpart for the clockwise direction, but similar significant differences presented for the delta, theta and alpha bands in the anticlockwise direction. Together, the results suggested that right-eye preferences for predatory behaviors exist in music frogs, and that the dynamics of EEG oscillations might underlie this right eye/left hemisphere advantage.

KEY WORDS: Visual lateralization, Right-eye preference, Predatory response, Electroencephalogram, Power spectra, Frog

INTRODUCTION

Lateralization refers to brain asymmetry and/or preferential use of one side of the body, which has been identified as widespread in vertebrates and certain invertebrates at both individual and population levels (Bisazza et al., 1998; Frasnelli, 2013; Frasnelli et al., 2012; Vallortigara et al., 2011, 1999; Vallortigara and Versace, 2017). Brain lateralization may enable brain function

specialization of the two hemispheres, enhance neural capacity (Levy, 1977; Rogers et al., 2004), leave the other side free to carry out extra functions (Denenberg, 1981), allow the brain's capacity to perform simultaneous processing various stimulus (Rogers et al., 2004) and increase individual fitness (Vallortigara, 2006). But the disadvantage is that predators could explore the regularity and predictability of behaviors that arise at the population level (Vallortigara, 2006). There are two main theories regarding brain lateralization (Besson et al., 2017). The 'brain's right hemisphere theory' presumes that the right hemisphere is mainly used to cope with information concerning novel events in response to which the animal may be in an intense emotional state (i.e. aggression, fear and escape behavior) and should respond rapidly, whereas the left hemisphere is used to categorize stimulus and process information that requires consideration of alternatives (MacNeilage et al., 2009; Prete et al., 2015; Rogers et al., 2013; Vallortigara and Rogers, 2005). Alternatively, the 'valence theory' presumes that the right hemisphere is preferentially used to process negative stimuli, whereas the left hemisphere primarily processes positive stimuli (Hook-Costigan and Rogers, 1998; Prete et al., 2015; Siniscalchi et al., 2013).

Visual lateralization, one of the brain specialization phenomena, is characteristic of numerous vertebrates such as fish (De Santi et al., 2001; Sovrano et al., 1999), amphibians (Delfour and Marten, 2006; Vallortigara et al., 1998), reptiles (Bonati et al., 2013; Csermely et al., 2011; Pellitteri-Rosa and Gazzola, 2018), birds (Güntürkün et al., 2000; Sandi et al., 1993; Vallortigara et al., 2001), mammals (Delfour and Marten, 2006; Thielges et al., 2011; von Fersen et al., 2000), non-human primates (Hook-Costigan and Rogers, 1995; Quresmini et al., 2014) and humans (Rogers, 2002b) when they process visual information. In general, right eye/left hemisphere and left eye/right hemisphere preferences exist for identifying prey or food from other non-food items and identifying the predator or some conspecific fight, respectively. For example, the chick (*Gallus gallus*) will be unable to categorize grains from pebbles when disrupting the glutamate treatment of the visual Wulst area of the left hemisphere, whereas the same treatment of the right counterpart has no effect (Deng and Rogers, 1997). Similarly, lesions in visual regions of the left or right hemisphere can affect the discrimination of prey and predators in anurans (Krauzlis et al., 2018). Interestingly, similar evidence has been provided that some invertebrate species such as the honeybee (*Apis mellifera*) learn a color stimulus better with their right eye (Letzkus et al., 2008) as well as an olfactory stimulus better with their right antenna (Rogers and Vallortigara, 2008; Rogers and Vallortigara, 2019). Moreover, eye preferences may be associated with stimulus characteristics such as complexity or novelty (Quaranta et al., 2007; Robins and Rogers, 2006), the subject's characteristics such as stress levels and vigilance (Hook-Costigan and Rogers, 1998), as well as their age or social environment (Besson et al., 2017; Hopkins and Bennett,

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List of abbreviations

EEG	electroencephalogram
LD	left diencephalon
LI	laterality index
LM	left mesencephalon
LSD	least significant difference
LT	left telencephalon
LVF	left visual field/left eye
PMMA	polymethyl methacrylate
RD	right diencephalon
RM	right mesencephalon
RT	right telencephalon
RVF	right visual field/right eye

1994). The preferential eye use for ecological activities such as scanning for potential prey or predators, processing visual information preponderantly through the left or right visual field, is dependent on specialized function of the left or right brain (Rogers et al., 2013; Vallortigara et al., 1999, 1998); however, the underlying dynamic neural mechanism of visual lateralization is unclear.

In anurans, studies on eye preferences show that foraging behaviors are preferentially controlled by the right eye, which is served by complementary specializations for the left hemisphere (Rogers, 2002b; Vallortigara and Rogers, 2005). In contrast to feeding behaviors, the left eye/right hemisphere is specialized for the sudden and possibly threatening changes within the environment, such as recognition of predator stimuli or novel stimuli (Andrew and Rogers, 2002; Lippolis et al., 2002). For example, right-eye preference for processing moving prey stimuli have been demonstrated in both frogs (Robins and Rogers, 2004, 2006; Vallortigara et al., 1998) and toads (Lippolis et al., 2002). Predatory behaviors in anurans are typically primitive and stereotyped mechanical (Rogers, 2002a). Moreover, the optic nerve fibers in the anuran visual system decussate almost completely so that visual information received by either eye is processed primarily by contralateral neural circuits of the brain (Fite and Scalia, 1976; Rogers, 2002a), although a number of commissures, such as tectal and hippocampal commissures, exist for proposed inter-hemispheric communications (Clairambault, 1976; Halpern et al., 1968; Rubinson, 1968; Scalia, 1976a,b). For these reasons, the anurans provide an excellent model to test the hypothesis that right-eye advantage in predatory behaviors is based on dynamic brain activities.

The electroencephalogram (EEG) allows broad canvassing of various brain areas and can be divided into several bands. EEG might be involved in different brain functions including sensory registration, perception, movement and cognitive processes related to attention, learning, memory and decision-making (Başar et al., 2000, 2001; Klimesch, 1999; Mazza and Pagano, 2017). Our previous studies show that EEG bands in the Emei music frog (*Nidirana daunchina*) differ substantially from those of humans, especially in the high frequency band (Fang et al., 2012a); however, auditory perception in this species is closely related to dynamic activities of various EEG bands (Fang et al., 2012b) and specific event-related potentials (Fan et al., 2019; Fang et al., 2015; Yang et al., 2018; Yue et al., 2017). Because discrete brain regions are specialized for different functions (Kandel et al., 2013), it seems reasonable to hypothesize that eye preferences related to predatory responses might be associated with different activity patterns of specific EEG bands and in specific brain areas.

The present study measured predatory responses in the music frog at both behavioral and electrophysiological levels in order to investigate whether eye preferences exist in this species and how the

visual central nervous system accommodates this preference. Specifically, the number of predatory responses and the power spectra of each EEG band were counted and analysed, respectively, when the prey stimuli were moved into the subject's left visual field (LVF) or right visual field (RVF). We predicted that: (1) presentations of moving prey stimuli in the RVF of the music frog would induce more predatory responses compared with presentations in the LVF because foraging behaviors in anurans are preferentially controlled by the right eye (Rogers, 2002b; Vallortigara and Rogers, 2005); (2) different power spectra of specific EEG bands would be exhibited between presentations of prey stimuli in the RVF and LVF because EEG bands interweave strongly with sensory and cognitive functions in the brain (Başar et al., 2001); and (3) the EEG power spectra of the left hemisphere would be higher than that of the right hemisphere during 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 (Clairambault, 1976; Halpern et al., 1968; Rubinson, 1968; Scalia, 1976a,b).

MATERIALS AND METHODS**Animals**

Forty-nine music frogs [*Nidirana daunchina* (Chang 1933); 27 males and 22 females] were collected from the Emei mountain area (29.60°N, 103.36°E, 1315 m above sea level) of Sichuan, China, for the present experiments. Forty-four (22 males and 22 females) and 14 (7 males and 7 females) frogs were used for the behavioral and electrophysiological experiments, respectively, nine of which were used for both types of experiment. The animals were separated by sex and housed in different opaque plastic tanks (45×35×30 cm, length×width×height), which were paved with mud and water so that the frogs could burrow and shelter themselves. The tanks were placed in a soundproof room under controlled temperature (23±1°C) and 70–80% relative humidity with a 12 h:12 h light:dark cycle (lights on at 08:00 h) using a fluorescent lamp. At the time of experiments, the mean±s.d. mass and length of the subjects regardless of sex were 8.8±1.5 g and 4.7±0.3 cm, respectively. The frogs were fed fresh live crickets every 3 days. All 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

All surgical procedures used in the present study have been described in detail in our previous studies (Fan et al., 2018a,b, 2019; Fang et al., 2012a,b; Yue et al., 2017). Briefly, the subjects were deeply anesthetized via water bath in a 0.15% (0.0015 g ml⁻¹) solution of tricaine methanesulfonate (MS-222) (Lalonde-Robert et al., 2012) and the optimum depth of anesthesia for surgery was determined by loss of the toe pinch response. Six cortical EEG electrodes composed of miniature stainless steel screws (0.8 mm in diameter) were implanted inside the frog skull and above the left and right sides of telencephalon (LT, RT), diencephalon (LD, RD) and mesencephalon (LM, RM), while the reference electrode (C) was implanted above the cerebellum (Fig. 1). All electrodes were fixed on the skull with dental acrylic. Each frog was housed individually for 6 days for recovery before performing further experiments. After all experiments were completed, the frogs were euthanized by overdose of MS-222 solution and the electrode locations were confirmed by injecting hematoxylin dye through the skull holes in which the recording electrode had been implanted previously.

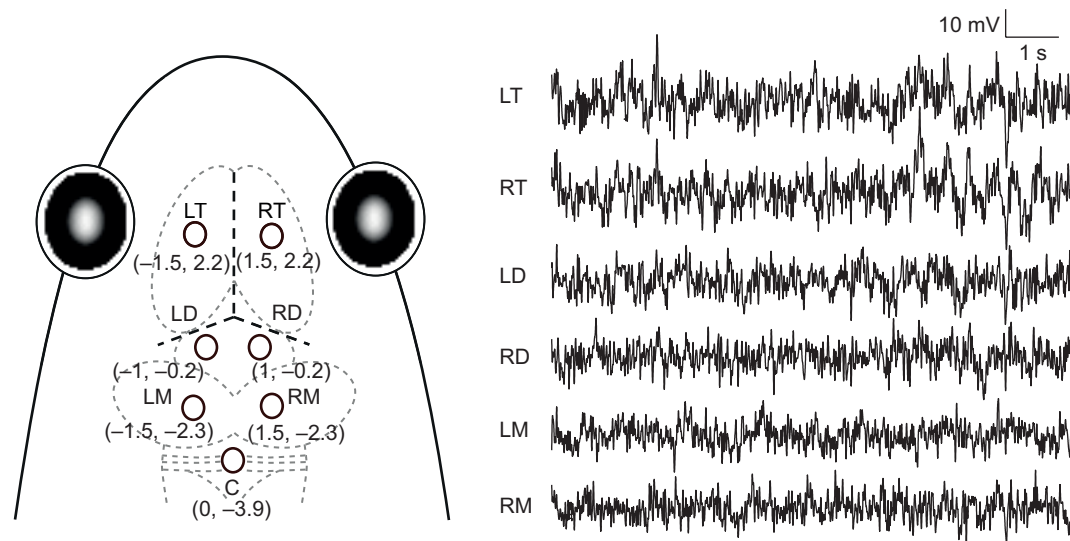


Fig. 1. Electrode placements and 10 s of typical EEG tracings for each channel. The intersection of the three dashed lines in bold in the frog head denotes the intersection of suture lines corresponding to lambda. LT, RT, LD, RD, LM and RM denote the left and right sides of telencephalon, diencephalon and mesencephalon, respectively; while C denotes the reference electrode implanted above the cerebellum.

Behavioral test apparatus

The design specifications for the test apparatus were based on previous research in toads (Burghagen and Ewert, 1983; Robins and Rogers, 2004; Wachowitz and Ewert, 1996). Briefly, a cylindrical cup (7 cm in diameter and 13 cm high) made of transparent polymethyl methacrylate (PMMA) was hung in the middle of a U-shaped frame made of transparent PMMA (Fig. 2). An electric turntable (20 cm in diameter and 5 cm high) was placed beneath the cup, and its motion parameters such as rotation direction and velocity could be controlled by PC via WiFi. A white plastic wafer (22 cm in diameter) was adhered to the bottom of the cup to minimize visual interference. A rod made of transparent PMMA was

bent to form a right angle and adhered onto a PMMA board, which was placed on the electric turntable. In addition, a white opaque plastic cylinder (40 cm in diameter and 30 cm high) surrounded all above components. A video camera with an infrared light source and motion detector (VSD-611H, Viesida Ltd, Shenzhen, China) was directly fixed on a tripod and positioned centrally approximately 1 m above the test apparatus to record behaviors of the animals.

Stimuli and test procedure

Live crickets (~1.5–2.0 cm in length) were used as prey stimuli (every live cricket for each frog) while fresh leaves of similar size to the crickets were used as the control. The stimulus was tethered using a white cotton thread and then was hung from the end of the rod (Fig. 2). The distance between the stimulus and the cup containing the animal was kept at approximately 3 cm.

The experiments were conducted in a soundproof and electromagnetically shielded chamber during which the background noise was 23.0 ± 1.7 dB, the temperature and relative humidity were $24 \pm 1^\circ\text{C}$ and 67–75%, respectively, and the light intensity was maintained at 0.07 lx. Before the behavioral test, the animal was fasted for at least 5 days. Then, it was placed in the cup containing water to a depth of approximately 1 cm. The stimulus was moved behind the frog using the rotating electric turntable. After the subject remained motionless for approximately 1 min, the stimulus circled the frog five times in the clockwise or anticlockwise direction at a constant velocity of $1.1 \text{ revolutions min}^{-1}$ (6.5 deg s^{-1}). After a 2-min break, the other direction was selected and the same procedure was conducted again. The rotation direction of the stimulus for the first five circles varied randomly among the subjects in order to control for possible biases. After the experiments were completed for each individual, the cup was washed and water was replaced for the next subject. The animal was fed live crickets and returned to its home tank.

For EEG signal recordings, the animal was placed in the cup and connected to the signal acquisition system (OmniPlex 64-D, Plexon, USA) for approximately 10 min habituation. The stimulus presentation was the same as in the behavioral experiments. A 100 Hz low-pass filter was used for EEG signals with the notch filter of the amplifiers set to eliminate possible interference at 50 Hz and improve the signal-to-noise ratio. The sampling frequency was



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

set to 1000 Hz. The experimenter pressed a button as soon as the prey-catching response of the animal was evoked so that a red LED outside of the white opaque plastic cylinder was illuminated and a trigger was sent to the signal acquisition system to synchronize the behavioral and EEG data.

Data processing

Similar to a previous study (Robins and Rogers, 2004), the predatory behaviors including turning of the body towards the prey stimuli and the tongue striking at it (hereafter referred to as ‘turns’ and ‘strikes’, respectively) were analyzed using frame-by-frame playback. Briefly, turns were scored as rotational movements of the frog’s body left or right towards the prey to bring it closer to the center of the binocular field and might be accompanied with tongue-striking, while strikes were scored as the tongue striking with ballistic projection at the prey. The other types of turns (i.e. avoidance behavior) were distinguished from predatory turns, and the prey-catching responses out of the visual field were not analyzed. In addition, prey-catching in the visual midline was not considered or analyzed (Vallortigara et al., 1998). Accordingly, the numbers of strikes, turns and strikes+turns for the LVF and RVF for each frog and each rotation direction were counted. Furthermore, laterality preferences for each subject were calculated using the laterality index (LI) (Bisazza et al., 2000), i.e. the ratio of the difference in numbers of predatory responses between the RVF and the LVF and the total number of predatory responses. Values significantly higher than 0 indicate a preference for the right eye, whereas values significantly lower than 0 indicate a preference for the left eye. In addition, we measured the strike angle and turn angle for each subject towards the prey using a screen ruler software package (MB-Ruler 4.0, Markus Bader Software Solutions, Iffezheim, Germany). The extent of the monocular and binocular visual fields in the horizontal plane at eye level was determined for 10 frogs (five males and five females) by measuring the angle at which the pupil could no longer be seen via an ophthalmoscope for both the ipsilateral and contralateral visual fields (Lippolis et al., 2002; Martin, 1984).

Prior to analyzing absolute power spectra, artifact-free 5 s EEG segments before the onset of every predatory responses were extracted. The data were filtered offline using a band-pass filter of 0.5–45 Hz and downsampled at 512 Hz. The segments were divided into 1 s epochs and each epoch was detrended (i.e. the linear trend was removed) using an algorithm that computes the least-squares fit of the data. Using Welch’s method with a Hamming window and 0.5 Hz resolution, the EEG absolute power spectra were calculated and transformed into a dB scale ($10 \times \log_{10}$) for each epoch, each channel, each visual condition (i.e. ‘out of sight’, LVF and RVF) and each EEG band, i.e. delta (0.5–5.5 Hz), theta (5.5–8.5 Hz), alpha (8.5–17 Hz) and beta (17–45 Hz), for the music frog (Fang et al., 2012a). The average absolute power spectra across the five epochs were calculated for further statistical analysis.

Statistical analyses

The normality of the distribution and the homogeneity of variance of the values were assessed by the Shapiro–Wilk *W*-test and Levene’s test, respectively. Because the behavioral data failed to meet the statistical assumptions, the Mann–Whitney *U*-test was used to test the differences in numbers of predatory responses (‘strikes’ and ‘turns’) between males and females, while the Wilcoxon signed rank test was conducted to explore the eye preferences of the subjects for predation. In addition, visual lateralization at group level was assessed via the one-sample Wilcoxon signed rank test.

For the EEG absolute power spectra, two-way repeated-measures ANOVA was carried out with the factors brain area (LT, RT, LD, RD, LM and RM) and visual condition (‘out of sight’, LVF and RVF). Because five male frogs did not respond to prey stimuli in LVF and there was no significant difference in the predatory responses between the sexes, sex was not included as a factor. 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 difference (LSD) test. Greenhouse–Geisser epsilon (ϵ) values were employed when the Greenhouse–Geisser correction was necessary. Estimations of effect size for ANOVAs were determined with partial η^2 (partial $\eta^2=0.20$ is a small effect size, 0.50 is a medium effect size and 0.80 is a large effect size) (Cohen, 1992). SPSS software (release 23.0) was employed for the statistical analysis, with $P<0.05$ considered as the significance level; $0.05<P<0.1$ was interpreted as marginally significant (Utts and Heckard, 2006).

RESULTS

The results of predatory behaviors

When the data were pooled regardless of the rotation direction of the stimuli, there was no visual bias for the control condition (fresh leaves) in both sexes ($Z=-2.010$, $N=15$, $P=0.888$ for males; $Z=-1.042$, $N=15$, $P=0.323$ for females), and there was no difference between the two sexes ($U=111.5$, $N=30$, $P=0.972$ for LVF; $U=95.5$, $N=30$, $P=0.479$ for RVF; Fig. 3A). No significant right-eye preference was found in the control condition for strikes ($Z=-1.000$, $N=30$, $P=1.000$), turns ($Z=0.595$, $N=30$, $P=0.564$) or strikes+turns ($Z=0.595$, $N=30$, $P=0.564$; Fig. 3B). There were more predatory turns compared with strikes for both the LVF and RVF ($Z=-4.312$, $N=30$, $P<0.001$ for LVF; $Z=-4.737$, $N=30$, $P<0.001$ for RVF; Fig. 3B). However, when live crickets were presented, there was a significant right-eye preference for both sexes ($Z=-2.612$, $N=22$, $P=0.009$ for males; $Z=-2.247$, $N=22$, $P=0.025$ for females), but there was no difference between sexes ($U=192.5$, $N=44$, $P=0.242$ for LVF; $U=195$, $N=44$, $P=0.267$ for RVF; Fig. 3C). The predatory responses for the RVF were significantly greater than those for the LVF for strikes ($Z=-2.246$, $N=44$, $P=0.025$), turns ($Z=-2.668$, $N=44$, $P=0.008$) and strikes+turns ($Z=-3.380$, $N=44$, $P=0.001$; Fig. 3D). In addition, there were more predatory turns than strikes ($Z=-5.666$, $N=44$, $P<0.001$ for LVF; $Z=-5.212$, $N=44$, $P<0.001$ for RVF).

When the rotation direction of the stimulus was considered, there was no visual bias for the control condition, although there were more predatory turns than strikes for both the LVF and RVF in the clockwise ($Z=-3.978$, $N=30$, $P<0.001$ for LVF; $Z=-4.165$, $N=30$, $P<0.001$ for RVF; Fig. 3E) and anticlockwise directions ($Z=-3.655$, $N=30$, $P<0.001$ for LVF; $Z=-4.026$, $N=30$, $P<0.001$ for RVF). However, there were significant right-eye preferences for presentation of live crickets in the clockwise direction for turns ($Z=-3.288$, $N=44$, $P=0.001$) and strikes+turns ($Z=-3.453$, $N=44$, $P=0.001$), but not strikes ($Z=-1.231$, $N=44$, $P=0.218$; Fig. 3F). In contrast, there was no significant bias in the anticlockwise direction ($Z=-1.589$, $N=44$, $P=0.112$ for strikes; $Z=-0.720$, $N=44$, $P=0.472$ for turns; $Z=-1.204$, $N=44$, $P=0.229$ for strikes+turns; Fig. 3F). Similarly, there were more predatory turns than strikes for both the LVF and RVF in the clockwise ($Z=-5.026$, $N=44$, $P<0.001$ for LVF; $Z=-4.873$, $N=44$, $P<0.001$ for RVF; Fig. 3F) and anticlockwise directions ($Z=-5.227$, $N=44$, $P<0.001$ for LVF; $Z=-4.631$, $N=44$, $P<0.001$ for RVF). LI was significantly greater than 0 for strikes ($P=0.013$) and strikes+turns ($P=0.011$; Fig. 3G)

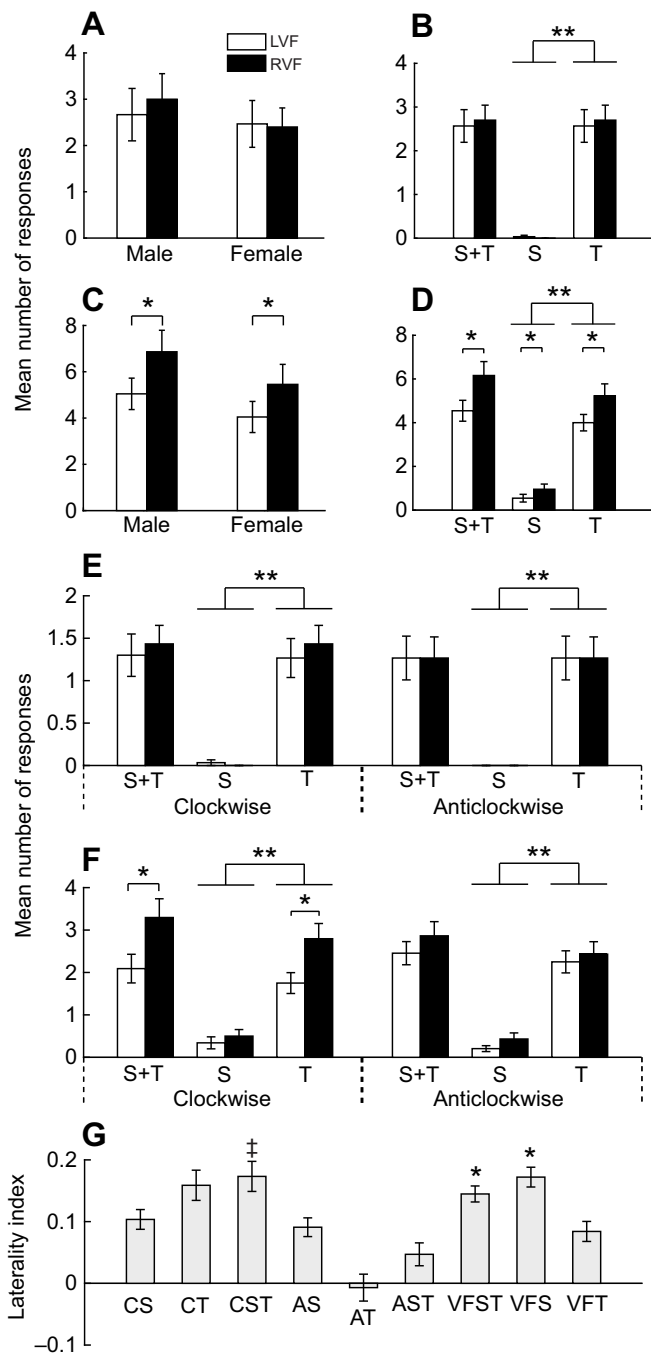


Fig. 3. The number of predatory responses according to sex, stimuli and rotation direction, and laterality index. (A,B) Number of predatory responses for the (A) two sexes and (B) different types of predatory responses when the control (leaf) was presented. (C,D) Number of predatory responses for the (C) two sexes and (D) different types of predatory responses when the prey stimuli (live cricket) were presented. (E,F) Number of predatory responses for the clockwise and anticlockwise directions under (E) control and (F) live cricket conditions. (G) Laterality index. LVF, left visual field; RVF, right visual field; S, number of strikes; T, number of turns; S+T, the sum of predatory responses; CS, number of strikes in the clockwise direction; CT, number of turns in the clockwise direction; CST, number of strikes and turns in the clockwise direction; AS, number of strikes in the anticlockwise direction; AT, number of turns in the anticlockwise direction; AST, number of strikes and turns in the anticlockwise direction; VFST, number of strikes and turns in visual fields; VFS, number of strikes in visual fields; VFT, number of turns in visual fields. Symbols denote significant and marginally significant differences (** $P < 0.001$, * $P < 0.05$, † $P < 0.1$).

for the pooled data regardless of the rotation direction, whereas LI was marginally significantly greater than 0 for strikes+turns ($P = 0.072$) in the clockwise direction. There was no significant difference for the other conditions. Moreover, the mean ipsilateral and contralateral visual fields were determined to be from -14 to 150 deg for the music frogs (Fig. 4).

Absolute power spectra for each EEG band

For the delta band (Fig. 5A,B), the main effect of brain area was significant for both the clockwise ($F_{5,35} = 9.827$, $P < 0.001$, partial $\eta^2 = 0.584$) and anticlockwise directions ($F_{5,40} = 11.759$, $P < 0.001$, partial $\eta^2 = 0.595$). There was no significant difference between both sides of telencephalon, diencephalon or mesencephalon for each visual condition (out of sight, LVF and RVF) in the clockwise direction, whereas the power spectra of the left diencephalon were significantly higher than those of the right counterpart for each visual condition in the anticlockwise direction ($P < 0.05$).

For the theta band (Fig. 5C,D), the main effect of brain area was significant in the clockwise direction ($F_{5,35} = 21.910$, $P < 0.001$, partial $\eta^2 = 0.758$), and the power spectra of the left diencephalon were significantly greater than those of the right counterpart for each visual condition ($P < 0.05$). For the anticlockwise direction, the main effect of brain area was significant ($F_{5,40} = 19.870$, $P < 0.001$, partial $\eta^2 = 0.713$), and the interaction between brain area and visual condition was also marginally significant ($F_{10,80} = 1.908$, $P = 0.056$, partial $\eta^2 = 0.193$). The simple effect analysis revealed that the power spectra of the left diencephalon were significantly higher than those of the right counterpart for the LVF and out of sight ($P < 0.05$); the power spectra of the left mesencephalon were significantly greater than those of the right counterpart for LVF ($P < 0.05$); the power spectra of the right diencephalon for the RVF were marginally significantly higher than those for the LVF ($P < 0.1$); and the power spectra of the right mesencephalon for the LVF were marginally significantly lower than those for out of sight ($P < 0.1$).

For the alpha band (Fig. 5E,F), the main effect of brain area was significant in the clockwise direction ($F_{5,35} = 47.435$, $P < 0.001$, partial $\eta^2 = 0.871$), and the interaction between brain area and visual condition was also significant ($F_{10,70} = 2.792$, $P = 0.006$, partial $\eta^2 = 0.285$). The power spectra of the left diencephalon were significantly higher than those of its right counterpart for the LVF ($P < 0.05$), and this was marginally significant for the RVF ($P < 0.1$); the power spectra of the left mesencephalon were significantly lower than those of its right counterpart for out of sight; and the power spectra of the left and right diencephalon for the RVF were marginally significantly higher than those of the left diencephalon for out of sight and those of the right diencephalon for the LVF, respectively ($P < 0.1$). For the power spectra of the alpha band in the anticlockwise direction, the main effect of brain area was significant ($F_{5,40} = 20.707$, $P < 0.001$, partial $\eta^2 = 0.721$), and the power spectra of the left diencephalon were significantly higher than those of the right diencephalon for each visual condition ($P < 0.05$).

For the beta band (Fig. 5G,H), the main effect of brain area was significant for the clockwise direction ($F_{5,35} = 21.824$, $P < 0.001$, partial $\eta^2 = 0.757$). Moreover, the interaction between brain area and visual condition was marginally significant ($F_{10,70} = 1.783$, $P = 0.080$, partial $\eta^2 = 0.203$). The power spectra of the left diencephalon were significantly higher than those of the right counterpart for each visual condition ($P < 0.05$). The power spectra of the left mesencephalon were marginally significantly higher than those of the right counterpart for the RVF and out of sight ($P < 0.1$). The power spectra of the right diencephalon for the LVF and RVF were marginally significantly higher than those for out of sight

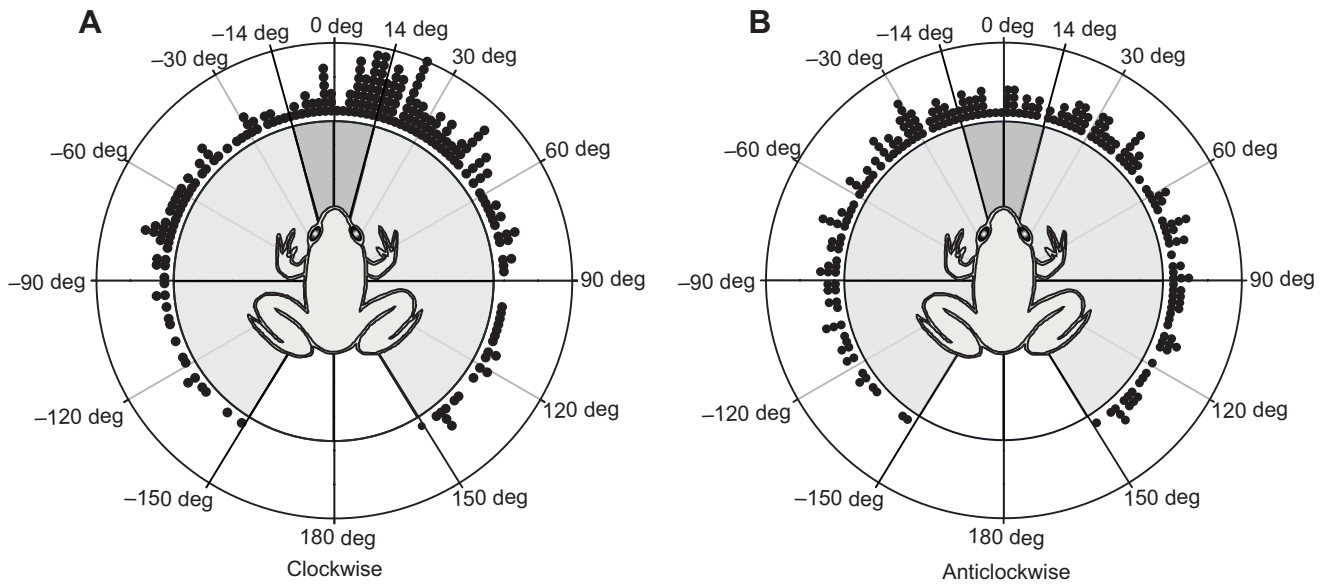


Fig. 4. Predatory responses with respect to visual fields when the prey stimuli were moved clockwise and anticlockwise. The positions of strikes and turns denoted by the angle of prey from the frog's midline were determined by marking the point of contact of the tongue on the hyaline cylindrical cup and the frog's body turning towards the rotated prey. 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 of the frog's visual fields. Note that a few responses for the prey stimuli out of sight are not shown.

($P < 0.1$) and the power spectra of the left mesencephalon for RVF were marginally significantly higher than those for LVF ($P < 0.1$). The power spectra of the telencephalon for the RVF were significantly higher than those for the LVF and out of sight ($P < 0.05$), although the difference between the RVF and LVF for the left telencephalon did not reach statistical significance. For the anticlockwise direction, the main effect of brain area was significant ($F_{5,40} = 20.491$, $P < 0.001$, partial $\eta^2 = 0.719$); however, there was no significant difference between the both sides of telencephalon, diencephalon or mesencephalon for each visual condition (out of sight, LVF and RVF).

DISCUSSION

The present results showed that: (1) when the live cricket was moved into the RVF clockwise, the number of predatory responses for the RVF were significantly greater than those for the LVF, but no significant difference of the number of predatory responses could be found for the control condition (leaf); (2) the power spectra of each EEG band for the prey stimuli moved into the RVF clockwise were greater than no stimuli in the visual field and stimuli in the LVF, although some of these differences did not reach statistical significance; and (3) overall, the power spectra of each EEG band with the exception of delta in the left diencephalon were significantly greater than that of the right counterpart for the clockwise direction, but similar diencephalic differences of EEG bands with the exception of beta were presented for the anticlockwise direction. These results were consistent with the hypothesis that the music frogs exhibited a right-eye preference for predatory behaviors and that the dynamics of EEG oscillations might underlie this right eye/left hemisphere advantage.

Right-eye preferences for predatory behaviors in the music frog

The present results showed that the music frogs exhibited a strong right-eye preference for predatory responses when the prey stimuli (live crickets) were moved into the RVF clockwise. These

results are consistent with previous studies in anurans such as *Bufo marinus*, *Bufo bufo* and *Bufo viridis*, which have shown that right-hemifield specialization for predatory responses exists when the subjects are tested individually with automated prey stimuli (Robins and Rogers, 2004; Rogers, 2002b; Vallortigara et al., 1998). However, no significant preference was exhibited when the leaf was presented, maybe because the leaf was lacking body segmentations, i.e. presence of legs or other appendages, compared with live crickets.

In general, the left hemisphere focuses attention to similarities and invariances between stimuli, in order to allocate stimuli into categories following rules established through experience or biological predispositions, while the right hemisphere responds to unexpected stimuli in environments (Rogers et al., 2013). The bias of the right eye to predatory responses found in anurans suggests that the anuran visual systems can respond to some basic or key aspects of prey stimuli that require the subjects to make considered decisions based on complex visual cues (Robins and Rogers, 2004). In contrast, simple prey stimuli consisting of black rectangular strips can induce a large number of predatory responses but not visual lateralization in toads (Robins and Rogers, 2004), consistent with the idea that neural circuits in the left hemisphere could be able to categorize and recognize prey stimuli using a series of criteria, and that analysis of simple prey stimuli may be located at a lower processing level in circuits (i.e. tectum) with an equivalent role and not the lateralization for predatory responses in anurans (Rogers, 2002b; Vallortigara, 2000). These findings, including the present results, suggest that the right eye/left hemisphere dominates the categorization and recognition of stimuli as well as the modulation of responses demanding consideration of alternatives (Rogers, 2002b; Vallortigara, 2000). Because a live cricket may be a positive stimulus for the music frog, the present results support both the 'brain's right hemisphere' theory, which presumes the right eye/left hemisphere is mainly used to categorize stimuli (MacNeilage et al., 2009; Rogers et al., 2013), and the 'valence theory', which presumes the left hemisphere primarily processes positive

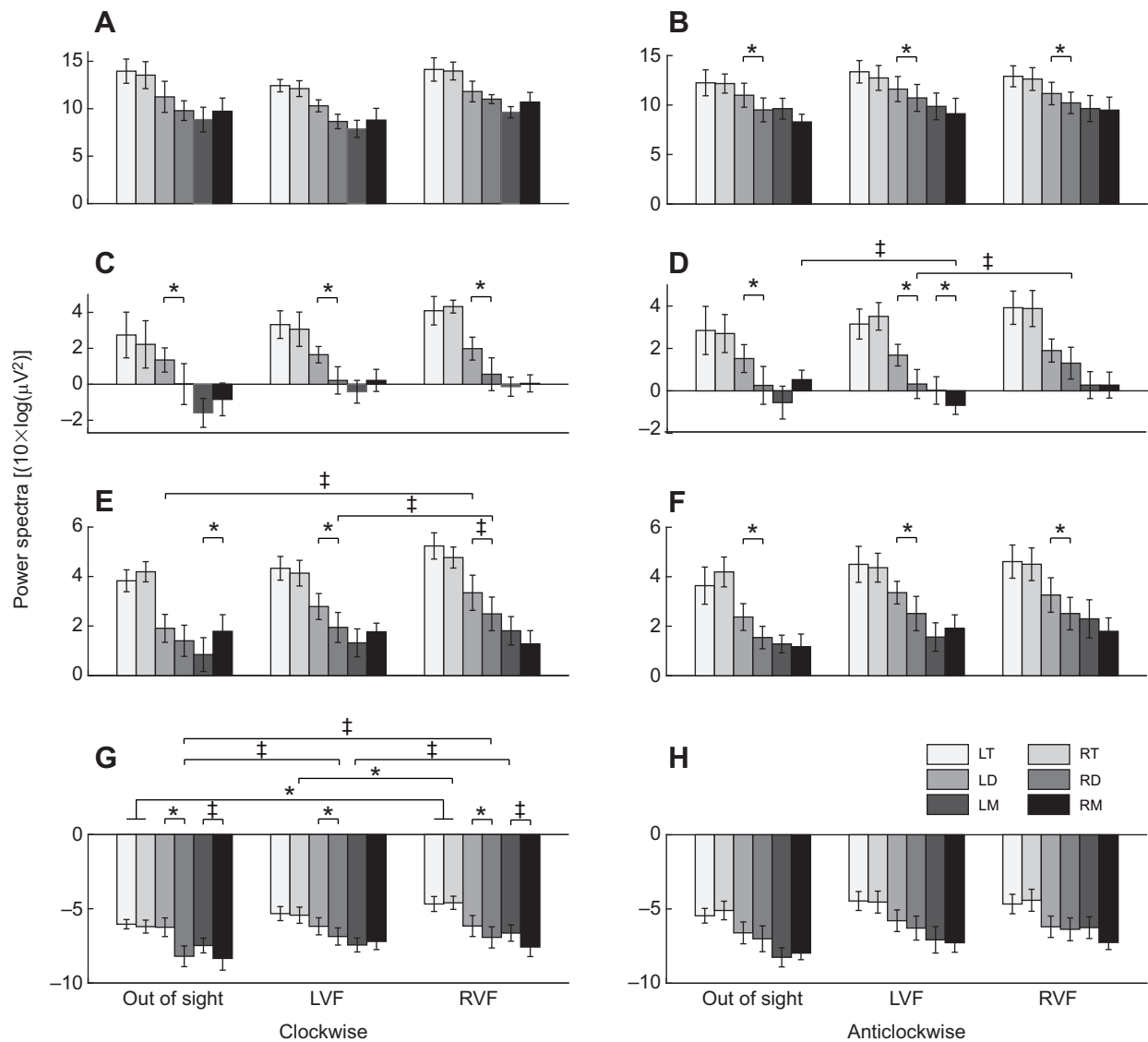


Fig. 5. Absolute EEG power spectra for each brain region and each visual condition (i.e. out of sight, LVF, RVF). (A,B) Delta, (C,D) theta, (E,F) alpha and (G,H) beta EEG bands; the two columns are for the clockwise (left) and anticlockwise directions (right). Symbols denote significant and marginally significant differences (* $P < 0.05$, ‡ $P < 0.1$) between the corresponding visual conditions or between different brain areas. LT, RT, LD, RD, LM and RM denote the left and right sides of telencephalon, diencephalon and mesencephalon, respectively. Data are means \pm s.e.m.

stimuli (Hook-Costigan and Rogers, 1998; Prete et al., 2015; Siniscalchi et al., 2013).

Visual lateralization appears in many vertebrates and certain invertebrates (Rogers et al., 2013). For example, right eye/left hemisphere dominance for prey has been found in cuttlefish (Schnell et al., 2016), fishes (Rogers, 2002b), anurans (Lippolis et al., 2002; Robins and Rogers, 2006), reptiles (Robins et al., 2005) and birds, including chicks (Mench and Andrew, 1986), pigeons (Güntürkün and Kesch, 1987) and quails (Valenti et al., 2003). In mammals, no research has specifically investigated lateralization of feeding responses (Rogers, 2002b), but the left hemisphere is specialized for responses akin to manipulation for a food reward in rats (Mittleman et al., 1988). Thus, it is reasonable to speculate that the right eye/left hemisphere preferences for prey responses is a common and relatively conservative brain function, consistent with the hypothesis that visual lateralization in animals may arise from a common lateralized ancestor. Although visual lateralization may be dangerous, i.e. the predator can exploit the predictability and

regularity of behaviors (Vallortigara, 2006), it is presumed to be able to perform qualitatively diverse types of processing simultaneously and enhance efficiency in cognitive tasks in both hemispheres (Rogers et al., 2004). Accordingly, visual lateralization can enhance the biological fitness of animals via selection pressures and favors the genes that promote the alignment of lateralization (Vallortigara, 2006). In other words, this lateralization may arise from genes related to the formation of asymmetries that have been selected under selection pressures.

Dynamic EEG oscillations may underlie visual lateralization for prey

The present results showed that the power spectra of alpha and beta bands for most brain areas were significantly greater when the prey stimuli were moved into the RVF clockwise compared with no stimuli in the visual field and stimuli in the LVF. In contrast, similar differences disappeared for the alpha and beta bands when the prey stimuli were moved into the RVF anticlockwise. Because the

subjects exhibited a strong right-eye preference for predatory responses when the prey stimuli were moved into the RVF clockwise, it seems reasonable to speculate that the dynamics of EEG bands with higher frequencies may play more important roles in visual lateralization for predatory behaviors.

Although alpha oscillations were historically considered to reflect an idling cortical state, recent experiments suggest that alpha rhythm serves as an attentional mechanism for focusing on relevant stimuli either by inhibition of unnecessary and/or conflicting processes to the task in hand or through increasing signal-to-noise ratios within the cortex (Klimesch, 2012). In other words, alpha rhythm can execute inhibitory function and also play a pivotal role in information processing that is closely connected to two fundamental functions of attention (suppression and selection) (Klimesch, 2012). The fact that brain processes related to the suppression are primarily connected with an increase in alpha amplitude indicates the inhibitory aspect of these oscillations (Händel et al., 2011; Jensen et al., 2012). Moreover, the alpha band may play a key role in the coalescence of brain activity at different frequencies (Klimesch, 2012). For example, the pair of alpha and beta rhythms may act as major carrier waves for attentional information (Wrobel, 2000). As important neuroanatomical features have been conserved during vertebrate brain evolution (Finlay et al., 2001; Northcutt, 2002), alpha would be expected to increase during a decision task, such as prey responses, which requires time to collect and process input information, as occurs in the RVF of animals. This speculation is consistent with a previous study on anurans that has shown that behavioral arousal (orienting behavior or prey-catching) in *Bufo regularis* and *Rana temporaria* results in an increase of alpha oscillations, particularly in the 10 to 22 Hz range (Laming, 1982).

Similarly, beta power increased when the prey stimuli were moved into the RVF clockwise compared with other conditions, which might reflect the demands of the rapid processing of visual signals for perception, such as recognition and classification of stimuli, attention to the prey and modulated accuracy of predator responses. Previous studies on humans and other animals have shown that changes in beta activities are associated with stimuli processing (Sehatpour et al., 2008) and visual attention (Gola et al., 2013; Siegel et al., 2008; Schall et al., 2007; Wrobel, 2000). The specific local increases in beta amplitudes during attentional tasks are positively relative with correct performance in both humans and other animals (Gola et al., 2013; Kamiński et al., 2012). Interestingly, increased beta signaling is correlated with anticipatory visual attention task in cats (Bekisz and Wróbel, 2003), in which increased beta band synchrony occurs in the entire dorsal pathway of visual system when the animals expect a predicted sensory event (Roelfsema et al., 1997). Furthermore, beta band oscillations in the monkey's sensorimotor network reflect the dynamics of decision making (Haegens et al., 2011), and lateralized changes in beta-band activity in motor and premotor cortex reflect a decision about an upcoming action already several seconds before it is executed in the human brain (Donner et al., 2009). Predatory responses are the decision outcome of the sensorimotor network in the brain, and in the present study, we found that increases in power output within the beta band matched closely with the dynamic properties of the visual signals presented in the RVF. Furthermore, significant differences of alpha and beta bands between the RVF and other conditions were found for the clockwise but not anticlockwise direction, which might reflect the fact that prey responses require time for the collection and processing of input information.

The tectum plays a necessary role in the initial prey-catching behaviors (Ewert, 1970), whereas the striatum may promote prey-catching by reducing pretectal inhibition of the tectum (Kang and Li, 2007). In frogs, the hypothalamus is the feeding center whereas the

thalamic binocular neurons and caudal thalamus are sensitive to moving visual objects (Ewert, 1971; Gaillard and Galand, 1979). Accordingly, striatum–pretectal–tectal circuits determine the prey recognition and localization properties, while pallium–thalamus–tectal connectivity means the brain can be sensitive to changes in internal state and to prior history of exposure to stimuli (Ewert, 1987; Ewert and Kehl, 1978; Ingle, 1973). Because the power of EEG bands in the left brain was significant greater than that in the right counterpart for most conditions, it seems reasonable to conclude that the dynamics of the lateralized EEG oscillations may result in right-eye preference in predatory responses in the music frog.

In summary, the present results suggest that a right-eye preference for predatory behaviors exists in the music frogs, and that the dynamics of EEG oscillations, especially at higher frequencies, might underlie this right eye/left hemisphere advantage.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

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

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