

RESEARCH ARTICLE

The biological significance of acoustic stimuli determines ear preference in the music frog

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ABSTRACT

Behavioral and neurophysiological studies support the idea that right ear advantage (REA) exists for perception of conspecific vocal signals in birds and mammals. Nevertheless, few studies have focused on anuran species that typically communicate through vocalization. The present study examined the direction and latencies of orientation behaviors in Emei music frogs (*Babina daunchina*) produced in response to six auditory stimuli emitted by a speaker placed directly behind the subjects. The stimuli included male advertisement calls produced from within burrow nests, which have been shown to be highly sexually attractive (HSA), calls produced from outside burrows, which are of low sexual attractiveness (LSA), screech calls produced when frogs are attacked by snakes, white noise, thunder and silence. For all sound stimuli except the screech, the frogs preferentially turned to the right. Right ear preference was strongest for HSA calls. For the screech and thunder stimuli, there was an increased tendency for subjects to move further from the speaker rather than turning. These results support the idea that in anurans, right ear preference is associated with perception of positive or neutral signals such as the conspecific advertisement call and white noise, while a left ear preference is associated with perception of negative signals such as predatory attack.

KEY WORDS: Right ear advantage, REA, Auditory perception, Conspecific calls, Mating strategy, Emotion

INTRODUCTION

Lateralization of function for neural structures has been identified in diverse vertebrate species at the individual and population levels (MacNeilage et al., 2009; Rogers and Andrew, 2002; Vallortigara et al., 2011). In mammals, auditory system lateralization has been shown to take the form of right ear advantage (REA) such that the organism tends to preferentially process conspecific vocal signals with the right ear while interspecific and environment sounds are preferentially processed using the left ear (Kimura, 2011; Vallortigara and Rogers, 2005). In principle, hemispheric lateralization could improve cognitive processing by allowing each hemisphere to specialize, thereby avoiding the simultaneous initiation of incompatible responses (Rogers, 2000; Rogers et al., 2004). Accordingly, animals with REA could theoretically process acoustic information more efficiently and thus respond more rapidly to environmental signals related to hunting

prey, predator activities and conspecific behaviors (Rogers et al., 2013; Vallortigara, 2006).

It has been reported that Japanese macaques (*Macaca fuscata*) best discriminate conspecific vocalizations using the right ear (Petersen et al., 1978). Similarly, mice best discriminate conspecific ultrasonic communication calls presented to the right ear (Ehret, 1987). Perhaps for this reason, rhesus monkeys (*Macaca mulatta*) preferentially orient their heads to the right side when conspecific calls are presented from a position directly behind the subjects, while turning to the left when presented with interspecific sounds (Hauser and Andersson, 1994). The same head orientation task has been conducted on sea lions (*Zalophus californianus*) (Böye et al., 2005), horses (*Equus caballus*) (Basile et al., 2009) and dogs (*Canis familiaris*) (Reinholz-Trojan et al., 2012; Siniscalchi et al., 2008), yielding results comparable to those obtained with rhesus monkeys.

Although REA has been reported in many species using head orientation preference, such tests have not as yet been carried out in anuran species despite the fact that anurans rely strongly on vocal communication. Right limb preferences in predator avoidance, body righting and nose scraping have been demonstrated behaviorally in anurans (Bisazza et al., 1996, 1997; Dill, 1977; Lippolis et al., 2002; Malashichev and Nikitina, 2002; Robins et al., 1998; Robins and Rogers, 2002, 2006; Rogers, 2002), while neural networks in the left hemisphere have been shown to play the predominant role in the production and perception of vocal signals (Bauer, 1993; Fang et al., 2012). Furthermore, left hemisphere dominance for vocalization/auditory perception has been shown to be related to right limb preference in humans (Knecht et al., 2000; Perlaki et al., 2013), non-human mammals (Fitch et al., 1993; Güven et al., 2003; Hopkins and Cantero, 2003; Peñe, 2002) and birds (Cynx et al., 1992; Ducker et al., 1986), especially for species utilizing vocal signals for social communication. Thus, it is reasonable to hypothesize that asymmetry for the production and perception of vocal signals is also related to limb preference in anurans and that lateralization of auditory perception would also be reflected in the behavior of these species.

In a previous study in the Emei music frog, *Babina daunchina* (Chang 1933), we investigated the effects of presentation of various acoustic stimuli including male advertisement calls on relative electroencephalogram (EEG) power in the delta, alpha and beta bands (Fang et al., 2012). *Babina* males produce advertisement calls from within hidden burrows whose resonant properties alter the acoustic properties of the calls (Chen et al., 2011; Cui et al., 2012, 2010). Phonotaxis experiments have shown that 70% of female *Babina* prefer calls produced from within the burrows, which are hence more highly sexually attractive (HSA) than those produced from outside the burrows, which are less sexually attractive (LSA) (Cui et al., 2012) and the male *Babina* prefer competing vocally with HSA calls rather than with LSA calls (Fang et al., 2014a). Electrophysiological studies show that relative power in the alpha, delta and beta bands declines or increases with time in the left but

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List of abbreviations

CRH	corticotrophin releasing hormone
EEG	electroencephalogram
HSA	high sexual attractiveness
LI	laterality index
LSA	low sexual attractiveness
MA	movement angle
MD	movement distance
REA	right ear advantage
TA	turn angle
WN	white noise

not right mesencephalon, with the most notable changes occurring during playbacks of HSA calls (Fang et al., 2014b). As the anuran midbrain receives auditory information derived primarily from the contralateral auditory nerve (Wilczynski, 1988; Wilczynski and Endepols, 2006), our results support the idea that REA is brought about by structural asymmetry superimposed with attention modulation (Fang et al., 2014b). However, behavioral evidence is required to test the theory that REA occurs in frogs.

The present study aimed to examine the behavioral REA responses of the Emei music frog. As animals habituate to repeated auditory stimulations using a given stimulus, such a procedure can produce biased results for ear-advantage measures (Siniscalchi et al., 2008). Furthermore, it has been shown that the population level of lateralization reflects the proportion of lateralized individuals (Ghirlanda and Vallortigara, 2004; Vallortigara, 2006). Thus, the population level rather than the individual level of lateralization was measured in the present study. As previous EEG studies have shown that conspecific calls most strongly activate the left hemisphere of animals with REA, we predicted that music frogs would turn generally rightwards in order to improve discrimination when hearing conspecific calls, with a stronger preference for HSA than LSA calls (Cui et al., 2012; Fang et al., 2014a). For other acoustic stimuli, we also predicted that (1) stimuli novel to frogs such as white noise (WN) would elicit either no turning or no orientation preference, and stimuli related to (2) explosive environmental sounds such as thunder or (3) sounds associated with predation would evoke either left turn movement or little preference, as reported in dogs (Reinholz-Trojan et al., 2012; Siniscalchi et al., 2008).

RESULTS

Data recorded from 46 frogs were analyzed. No differences were found among the eight exemplars of the HSA calls, LSA calls and thunder stimuli or between the two sexes. Thus, all data for each type of stimulus were pooled for further analysis. The turning angles induced by the HSA call were generally larger than those induced by other stimuli; however, there were no significant differences in movement angles and movement distances among stimuli (not shown).

Different stimulus types induced different response patterns

Frogs responded to the acoustic stimuli mostly by turning *in situ* or moving away; rarely did frogs not respond to an acoustic stimulus (Fig. 1). Overall, there were no significant differences in response numbers between turning *in situ* and moving away, although there were slightly more frogs that were more likely to move away than turn *in situ* in response to the screech and thunder stimuli. The reverse tendencies were observed for the other stimuli. The total number of active responses was greatest to the conspecific calls (i.e. the HSA and LSA calls) among all stimuli, but the difference was not statistically significant.

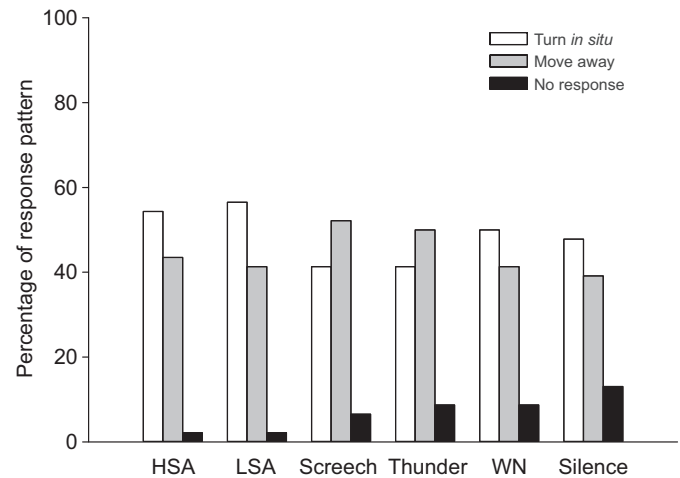


Fig 1. The percentage of behavioral response patterns to different stimuli.

'Turn *in situ*' was scored if the frog turned around but moved away from the initial position no more than one snout–tail length. 'No response' was scored if the frog stayed in the original position without any action until the end of the trial. 'Move away' was scored if the frog moved more than one snout–tail length from the initial position. HSA, high sexual attractiveness advertisement call; LSA, low sexual attractiveness advertisement call; WN, white noise.

Behavioral response lateralization varied between stimuli

Lateralization of turning *in situ* is shown in Fig. 2. Frogs preferred turning to the right side more than to the left in response to the HSA call (a single sample Chi-square test: $\chi^2=6.760$, $P<0.05$). Although more frogs turned right than left in response to the LSA call, this difference was not significant. The tendency to turn rightwards was greater for HSA than for LSA calls despite the fact that the difference was not significant (Fisher's exact test: $P>0.05$, two-sided). The frogs showed no significant preference to turn leftwards in response to the screech stimulus (a single sample Chi-square test: $\chi^2=1.316$, $P>0.05$), while there was a significant difference in the number of frogs turning leftward/rightward in response to the screech and leftward/rightward in response to HSA calls (Fisher's exact test: $P<0.05$, two-sided). Frogs showed a slight tendency to turn rightwards in response to the thunder and WN stimuli.

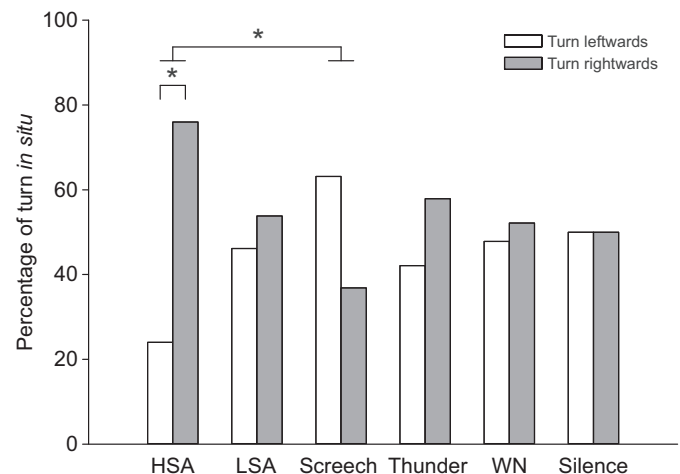


Fig 2. The percentage of turn *in situ* responses to different stimuli after correction (rectification) from the baseline of responses to silence. For details, see Materials and methods. Asterisks denote that there are significant differences in turning bias between different cases ($P<0.05$). HSA, high sexual attractiveness advertisement call; LSA, low sexual attractiveness advertisement call; WN, white noise.

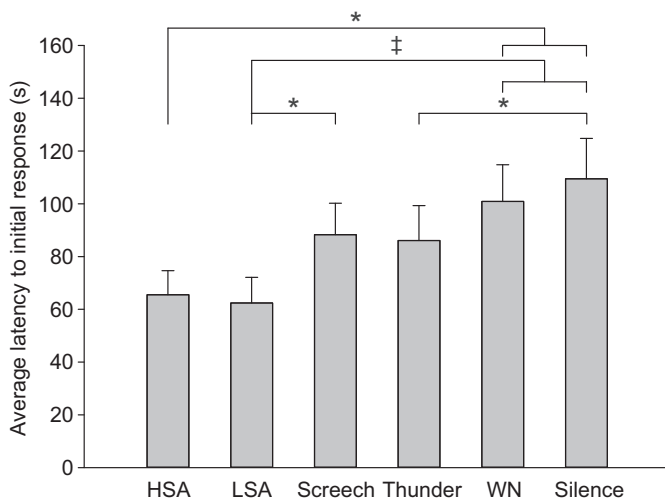


Fig 3. The mean (+s.e.) of response latencies for each stimulus. The bars represent response latencies between the onset of stimuli playback and the frogs' first responses. Asterisks and double daggers denote significant differences of the latency values among different stimuli (* $P < 0.05$ and † $P < 0.01$). HSA, high sexual attractiveness advertisement call; LSA, low sexual attractiveness advertisement call; WN, white noise.

Response latencies were shorter for advertisement calls

Figs 3 and 4 show response latencies to the stimuli and corresponding behavior scores, respectively. A tendency to respond to a stimulus with a shorter latency was associated with a higher behavior score. To be more specific, the HSA calls elicited a significantly shorter response latency than WN (Wilcoxon signed rank test: $Z = -2.355$, $N = 46$, $P < 0.05$) and silence (Wilcoxon signed rank test: $Z = -2.229$, $N = 46$, $P < 0.05$) while the HSA behavior score was higher than those for the screech call (Wilcoxon signed rank test: $Z = -2.216$, $N = 46$, $P < 0.05$), thunder sound (Wilcoxon signed rank test: $Z = -1.961$, $N = 46$, $P < 0.05$) and silence (Wilcoxon signed rank test: $Z = -2.393$, $N = 46$, $P < 0.05$). The response latency elicited by the LSA call was significantly shorter than those elicited by the screech (Wilcoxon signed rank test: $Z = -2.267$, $N = 46$, $P < 0.01$), WN (Wilcoxon signed rank test: $Z = -2.693$, $N = 46$, $P < 0.01$) and silence (Wilcoxon signed rank test: $Z = -2.850$, $N = 46$, $P < 0.05$) stimuli. In addition, the average behavior score was higher for the LSA call but not significantly so. The silence stimulus was associated with the longest response latency, being significantly longer than that associated with the thunder stimulus (Wilcoxon signed rank test: $Z = -2.399$, $N = 46$, $P < 0.05$). The behavior score for silence was lower than for all other stimuli.

DISCUSSION

Although Hylidae species can turn their heads relative to their bodies to some extent (Caldwell and Bee, 2014), music frogs only rotated the body or moved around in response to external stimuli in our experiment. Changing the position of the ears relative to a sound source enables animals to optimally localize sound sources by utilizing the resulting variations in either the amplitude or phase of tympanum vibrations between the two ears (Christensen-Dalsgaard, 2005). Thus, turning of the body *in situ* in music frogs was assumed to be the functional homolog to head turning in mammals and birds, and was taken as an indication of lateralization for fine auditory stimulus processing. However, the generalizability of the orienting-asymmetry paradigm and the relationship between orienting asymmetries and brain lateralization for acoustic processing is still being evaluated (Teufel et al., 2010). A goal of the present

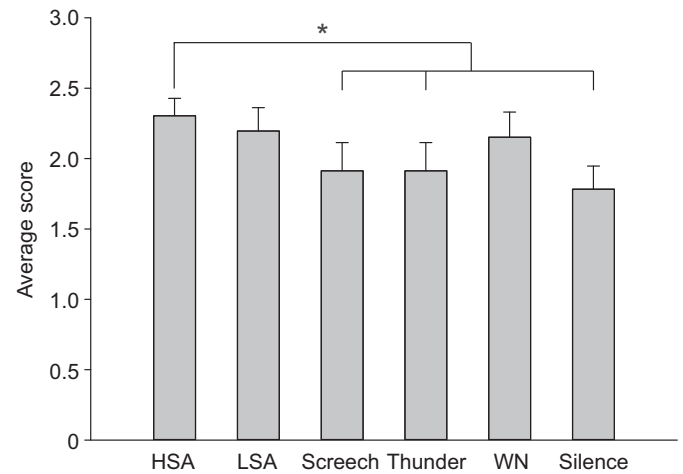


Fig 4. The mean (+s.e.) of overall behavior scores for each stimulus. The number of either turn *in situ* or move away responses the frog produced to a stimulus was counted and regarded as the behavior score of each subject to each stimulus. These values were summed over all subjects for each stimulus to calculate an average behavior score. Asterisks denote significant differences of the behavioral scores among various stimuli ($P < 0.05$). HSA, high sexual attractiveness advertisement call; LSA, low sexual attractiveness advertisement call; WN, white noise.

study was to contribute to the evaluation of this paradigm. Explication of anuran vocal/auditory lateralization should entail behavioral tests for side preferences in conjunction with study of the physiological processes directly reflecting ongoing brain activities, such as EEG and/or positron emission tomography (PET). Pertinent to this, we previously conducted an electrophysiological study demonstrating a right ear/left brain advantage in auditory processing in this species (Fang et al., 2014b), supporting the present behavioral results.

REA behaviors correspond to known neural lateralization patterns

Twenty-five frogs turned *in situ* when HSA calls were presented from a speaker immediately behind them, 76% of which turned rightwards. This rightward bias is comparable to results of head orientation studies in other vertebrates (Bøye et al., 2005; Basile et al., 2009; Hauser and Andersson, 1994; Reinholz-Trojan et al., 2012; Siniscalchi et al., 2008) and supports the idea that among land vertebrates, most individuals orient the right side of the head towards sound sources when listening to conspecific calls. Recent work on sound localization behavior in gray treefrogs, which differ from music frogs in both habitat and phylogenetic position (Alexander Pyron and Wiens, 2011), showed no consistent tendency to turn rightwards for females in response to male advertisement calls, in either 0 or 180 deg sound presentations (Caldwell and Bee, 2014). This may be attributed to the fact that music frogs live on the ground and prefer responding to sounds varying in azimuth in contrast to arboreal frogs, which must process sounds varying both azimuthally and vertically.

Previous electrophysiological studies in the Emei music frog have supported the idea that lateralization of processing of conspecific vocal signals occurs in this species (Fang et al., 2011, 2014b, 2012). These studies report that power in the EEG bands of the left hemisphere, especially of the left mesencephalon, tends to be greater or to change significantly compared with that of the right in response to conspecific call stimulation. As auditory pathways in anurans tend to project information most strongly to the contralateral midbrain

(Wilczynski and Endepols, 2006), the behavioral results of the present study indicating an REA for all stimuli except the screech are consistent with these electrophysiological studies.

Cerebral lateralization of auditory processing has been demonstrated in anuran (Bauer, 1993), avian (Cynx et al., 1992) and mammalian (Heffner and Heffner, 1995) species using the lesion method. Lesions of the left hemisphere reduce the ability to discriminate and/or produce conspecific sounds to a greater degree than lesions of the right hemisphere. Neurophysiological studies in bats have shown that the left hemisphere neurons are more responsive to social calls while those of the right are more responsive to navigational signals (Kanwal, 2012). Theoretically, neural lateralization would improve information processing efficiency by providing specialized analysis within each hemisphere, thereby enhancing the ability of land vertebrates to make critical decisions related to mating or feeding in dangerous environments (Rogers et al., 2004). Our behavioral and electrophysiological studies of the lateralization of auditory perception in anurans provides experimental evidence in support of the idea that hemispheric asymmetry in processing cues related to complex perception originated at an early stage in vertebrate evolution (Ocklenburg et al., 2013; Vallortigara, 2000; Vallortigara et al., 1999).

Mating strategy influences the response to advertisement calls

Both HSA and LSA advertisement calls elicited more body turning to the right than to the left; however, only HSA calls elicited a statistically significant bias in the rightward direction in this study. Nevertheless, LSA calls evoked behavioral response patterns that differed from those of the non-biological thunder and WN stimuli (see Fig. 1). These results are consistent with those of previous phonotaxis experiments, which showed that when HSA and LSA calls were played back antiphonally from both sides of a test chamber to female music frogs, more than 70% of the subjects approached the speaker broadcasting HSA calls (Cui et al., 2012). The results of the present study are also consistent with previous behavioral tests of male vocal competition. Fang et al. (2014a) showed that when male frogs listen to an HSA and an LSA call presented alternately, the male subjects preferred competing vocally with the HSA calls rather than the LSA calls. Therefore, the sexual attractiveness of the stimuli, which plays an important role in female mate selection and male vocal competition, also affects rightward turning for both males and females, consistent with the idea that the neural resources involved in processing signals with high biological significance differ between the hemispheres.

As animals are able to assess the costs and benefits of competing for resources (Arnott and Elwood, 2008), it is reasonable to hypothesize that music frogs would pay less attention to males producing the LSA call because such individuals lack a nest and would therefore be less valued targets for mating or competition (Kirkpatrick et al., 2006). Such a strategy would thus enable males to allocate energy and attention resources toward more valued targets (Greenfield and Rand, 2000) as well as enable males to reduce the predation risk that usually accompanies reproductive activities (Magnhagen, 1991; Reznick, 1992), which would thereby increase fitness.

Fear as a motivator of the frogs' behavior

The screech stimulus evoked a tendency to turn leftwards and was associated with longer response latencies than for the HSA or LSA calls despite the fact that the screech is also a conspecific call. Similar response patterns have been shown in dogs, which turn their

heads left in response to playbacks of barking stimuli (Reinholz-Trojan et al., 2012) and displays of a picture of a snake (Siniscalchi et al., 2010). These authors pointed out that this behavioral pattern appears to reflect activation of the left ear/right hemisphere system consistent with the fact that the right hemisphere is specialized to process stimuli evoking negative affect (Vallortigara and Rogers, 2005).

Emotion can motivate behavior (Zhu and Thagard, 2002) and fear is a common emotion linked to behaviors elicited by potential danger (Faure et al., 1983; Galac and Knol, 1997; Prather et al., 2001). The amygdaloid complex and right hemisphere pallial structures are believed to be involved in processing affective stimuli in mammalian and avian species (Andrew, 1983; Crowne et al., 1987; Davidson and Tomarken, 1989; Denenberg, 1981; Fernández-Carriba et al., 2002; Slotnick, 1973; Wallez and Vauclair, 2011). Although the frog's telencephalon is not as well differentiated compared with that of mammals and birds (Butler and Hodos, 2005), limbic system structures that appear homologous to the amygdala and hippocampal formation of mammals have been described in frogs (Bruce and Neary, 1995), which possess ascending and descending connections comparable to the corresponding structures of mammals (Laberge et al., 2006).

Yao et al. (2004) studied the distribution of corticotrophin releasing hormone (CRH)-like peptides in the clawed frog (*Xenopus laevis*) brain, which conform to the distribution of CRH-positive neurons in mammals and are hypothesized to serve similar functions. It is notable that when clawed frogs are stressed by shaking, the concentration of CRH-like peptides in the medial amygdala significantly increases, similar to the effect of stressors in the mammalian amygdala. In addition, functional studies indicate that the modulation of CRH within the hypothalamic-pituitary-adrenal axis is similar in diverse vertebrate species (Denver, 2009).

Comparative neuroanatomical and immunohistochemical studies support the idea that frogs can process affective stimuli, especially those associated with fear evoked by predator avoidance (Dill, 1977; Lippolis et al., 2002). Nevertheless, affective behavior is more limited in frogs than in birds and mammals, as indicated by studies reporting the lack of an emotional fever response in amphibians (Cabanac and Cabanac, 2004; Cabanac, 1999). As the screech call used in our study was recorded during a snake attack, it is reasonable to categorize this screech call as a defensive call that would help frogs avoid predation (Toledo et al., 2014). Therefore, the screech call serves as a warning of potential predators and also transmits a negative emotion (e.g. fear and distress).

Fear activates the amygdala complex and results in freezing responses in many prey animals (Ryan, 1985). Consistent with this idea, a longer response latency was associated with the screech call stimulus. Moreover, frogs either moved directly away or turned to the left side in response to the screech. These behaviors are consistent with the idea that the screech signals danger, further processing of which is best served by the left ear/right hemisphere system, which, in mammals, is functionally important for mediating withdrawal behavior, behavioral inhibition and negative emotion (Davidson, 1984a,b; Davidson et al., 1990; Quaranta et al., 2007; Siniscalchi et al., 2013; Sutton and Davidson, 1997). In this way, the subjects are able to rapidly make an escape action decision based on trade-offs between the costs and benefits (Broom and Ruxton, 2005; Cooper and Frederick, 2007).

In summary, the REA and corresponding behaviors exist in Emei music frogs and appear comparable to those described in other vertebrates. The existence of a right ear preference for advertisement calls and a left ear preference for calls signaling danger supports the idea that the frogs' REA behavior is modulated by mating strategies as well as negative emotions such as fear.

MATERIALS AND METHODS

Animals

A sample size of 48 music frogs was used based on sample sizes utilized in previous lateralization studies in anuran (Lippolis et al., 2002; Vallortigara et al., 1998) and mammalian species (Hauser and Andersson, 1994; Reinholz-Trojan et al., 2012). The frogs were captured by hand with a filter gauze from several ponds in Emei Mountain area (29.60°N, 103.36°E, elevation of 1315 m above sea level), Sichuan, China, from 15 to 20 July 2013, during their breeding season. Animals were equally divided into two waterproof polyamide boxes (48×29 cm and 28 cm deep) containing water (1 cm depth) with a piece of tile fixed on the bottom. The boxes were covered with ventilated dark cloths and transferred to the laboratory in Chengdu by car in about 6 h (a distance of ~160 km) where the car temperature was maintained at 20°C. No frog died during the transportation. The music frog is a common regional species, which can be found in virtually all ponds in the Emei area (Fei et al., 2012). There was no evidence of population fluctuation in the capture sites based on previous studies carried out over the last several years (Cui et al., 2012; Fang et al., 2014a).

In the laboratory, the frogs were separated by sex and housed in three opaque plastic tanks (45×35 cm and 30 cm deep). One tank contained 14 females and two tanks contained 17 males each. The opaque plastic material allowed partial transmission of light. Each tank contained about 3 cm depth of water with about 5 cm of mud in height around the walls so that the frogs could make or find shelters themselves. The tanks were placed in a room under controlled temperature (23±1°C) and relative humidity (70–80%) with a 12 h:12 h light:dark cycle (lights on at 08:00 h) using a fluorescent lamp. The animals were fed live crickets (bought from a pet food shop) every 3 days according to our previous study (Fang et al., 2011, 2014b, 2012; Yang et al., 2014). About 50 crickets were provided to each box, not all of which were eaten. The leftover crickets were cleaned out after 24 h.

Each subject was moved gently to the playback experiment chamber. After each test, the animal was released into a box (40×28 cm and 22 cm deep) containing water and mud (eight individuals maximum per box) and fed as in the home tanks. All individuals in each tank were returned to their home tank after finishing all trials (generally 4 or 5 days after the first trial). Every frog completed the playback testing within 2 h and no frogs died during the experiment period.

After the experiment, no deaths occurred and the frogs were used for further electrophysiological experiments in order to minimize the influence on natural populations. The health of the frogs was monitored by observing feeding and motion patterns on the feeding day (i.e. once every 3 days), and their mass was stable throughout the experiment period.

All experiments were in accordance with the Law of the People's Republic of China on the Protection of Wildlife and approved by the Chengdu Institute of Biology Animal Care Committee (permit number: 2011–015).

Apparatus and stimuli

A soundproof and electromagnetically shielded chamber (the background noise equaled 23.0±1.7 dB) was used for conducting the experiments. A plastic plate (radius 22.5 cm) filled with wet mud was placed in the center of the chamber. A circle, whose radius was 75 cm from the center point of the chamber, demarcated the area where a speaker (SME-AFS, Saul Mineroff Electronics, NY, USA) was located (Fig. 5). A pellucid plastic cover with small vents was placed on the center of the plate. The plastic cover could be lifted quickly via a cotton cord connected to the top of the cover, which was extended to the outside of the chamber through a pulley fixed on the ceiling and a hole in the wall so that the experimenter could

manipulate it. A video camera with an infrared light source (VSD-611H, Viesida Ltd, Shenzhen, China) and a microphone (ME66, Sennheiser, Wedemark, Germany) were mounted on a tripod and positioned over the center of the chamber using an extensional arm so that audio and video recording of the subjects' movements and vocalizations could be monitored. The sound pressure level of the speaker output was adjusted to 70 dB measured at a distance of 1 m from the speaker, producing a 1000 Hz pure tone using a sound level meter (AWA 6291, Aihua Instruments, Hangzhou, China). As the subjects changed position within the cover from time to time, the speaker was placed into the chamber by the experimenter at the beginning of each trial such that it was positioned immediately behind the subject as shown in Fig. 5.

Six types of acoustic stimuli were recorded and synthesized: an HSA call, an LSA call, a screech call, thunder, WN and silence (Fig. 6, silence is not shown). A pair of HSA and LSA calls was defined as recordings obtained from the same individual in the burrow and open field, respectively, and eight such pairs of individual advertisement calls each consisting of four notes were chosen from the dataset of our laboratory. Eight different sounds of thunder each of less than 4 s duration were downloaded from the Internet (<http://soundbible.com/> and <http://www.partnersinrhyme.com/>). The screech call was recorded during a snake attack. WN was synthesized with Adobe Audition, and its duration was the average of the durations of all HSA and LSA calls, containing a 50 ms period with sinusoidal rise–fall characteristics to avoid transients. The silence stimulus was also made with Adobe Audition as a neutral control (not shown in Fig. 6).

Therefore, the stimulus set consisted of eight exemplars of an HSA call, LSA call and thunder sound in order to control for the possible effects of pseudoreplication (Hurlbert, 1984; McGregor, 2000; McGregor et al., 1992). Only one exemplar each for the screech call, WN and silence stimuli was used. All stimuli except for silence were equalized for intensity (65 dB SPL; measured 1 m from the adjusted speaker).

Each experimental trial consisted of a series of repeating acoustic stimuli selected from one of the six stimulus types described above and selected randomly from our database. These stimuli differed in duration; however, the inter-stimulus intervals equaled 3.3 s, the average period between two successive advertisement calls produced by music frogs in the field (Fang et al., 2014a). Each trial lasted 5 min or until the subject moved away

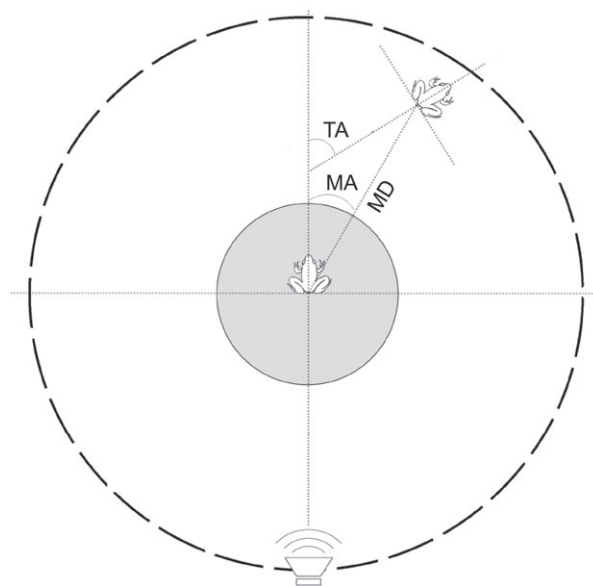


Fig 5. Diagrammatic representation of the experimental setup and the parameters measured in the present study. The dashed circle shows the zone in which the speaker was placed. The shaded circular area represents the plate. TA, turn angle; MA, movement angle; MD, movement distance. This example illustrates a response in which the frog moved away from the speaker with body turning. In cases in which the frog moved less than its snout–tail length, MA and MD were both regarded as zero (see Materials and methods).

from the plate as described below. Thus, for each trial, one of the eight exemplars for the HSA, LSA and thunder stimuli was selected randomly from the database or the silence, WN or screech call stimuli were presented. An entire experiment block consisted of six trials of stimulus playbacks in random order in which each stimulus was used once for a specific individual subject.

Test procedure

Behavioral testing was performed at 20:30 h–24:00 h and at 03:30 h–07:00 h the next day. Previous studies have shown that the frogs are active during these times of the night (Yang et al., 2014). Each subject was placed under the cover and allowed to move freely inside. After the subject remained still for more than 3 min, the speaker was placed carefully and slowly behind the subject, aligned with the snout–tail axis of the animal as shown in Fig. 5. One of the six stimuli was chosen randomly and presented to the subject as soon as the cover was lifted. The trial ended when the subject moved away from the plate or when the 5 min playback ended. At this point, the speaker was removed and the subject was put back under the cover. The procedure was repeated until all stimuli had been presented.

Data processing

The frogs' reactions to each stimulus were analyzed offline based on the video recordings, with the stimulus type blind to the investigator scoring the behavior. Three response patterns were identified: no movement, turning in place (turn *in situ*) and movement away from the speaker. The last two behaviors were identified as active responses. Other reactions (e.g. blinking or scratching) were excluded from further analysis because these responses were observed rarely, less than 10 times throughout all trials. Subjects that did not respond to any of the six stimuli were excluded in the statistical analyses. The number of trials for which each subject's first response to each stimulus type was to turn *in situ*, move away from the speaker or exhibit no response was counted manually by the experimenter. The orientation response of turning *in situ* was identified by the experimenter if the frog turned around but moved less than its snout–tail length away from the origin. The response of moving away was scored if the subject jumped more than a distance of one snout tail length away from the center (see Fig. 5). The first

reaction in each trial was taken to reflect the frog's preferential response to the stimulus; other actions were counted for computing an overall behavioral score as described below.

We used the response to silence as a baseline for determining orientation bias for individual subjects in the absence of any acoustic stimulation in order to reduce the potential impact of internal factors. The rectified data (i.e. data corrected for bias) for all stimuli except silence were statistically tested. For each of the other five stimuli, laterality preferences for each subject were calculated as follows. (1) A laterality index (LI) for each stimulus type was calculated by the formula:

$$LI = \frac{L - R}{L + R}, \quad (1)$$

where L and R designate the number of trials in which the subject oriented to the left and right, respectively (Siniscalchi et al., 2008). (2) The LI_r (laterality index after being rectified or corrected for bias) for each stimulus could be calculated using the formula:

$$LI_r = LI - LI_s, \quad (2)$$

where LI_s is the laterality index of silence. (3) LI_r could also be represented by the following formula:

$$LI_r = \frac{L_r - R_r}{L_r + R_r}, \quad (3)$$

where L_r and R_r designate the number of subjects who oriented to the left and right, respectively, after bias rectification. (4) As there were few trials in which the subjects exhibited no response to a given stimulus, it was reasonable to consider that $L_r + R_r$ and $L + R$ were basically equal. Therefore, $L_r + R_r$ and LI_r were known so that $L_r - R_r$ could be solved from Eqn 3 and then L_r and R_r for each stimulus could be calculated from the linear equations. A few subjects with no response to all stimuli were excluded in the rectification calculations (bias correction).

We measured the turn angle (TA), movement angle (MA) and movement distance (MD) for each subject's first response to each stimulus (see Fig. 5) using a screen ruler software package (MB-Ruler 4.0, Markus Bader

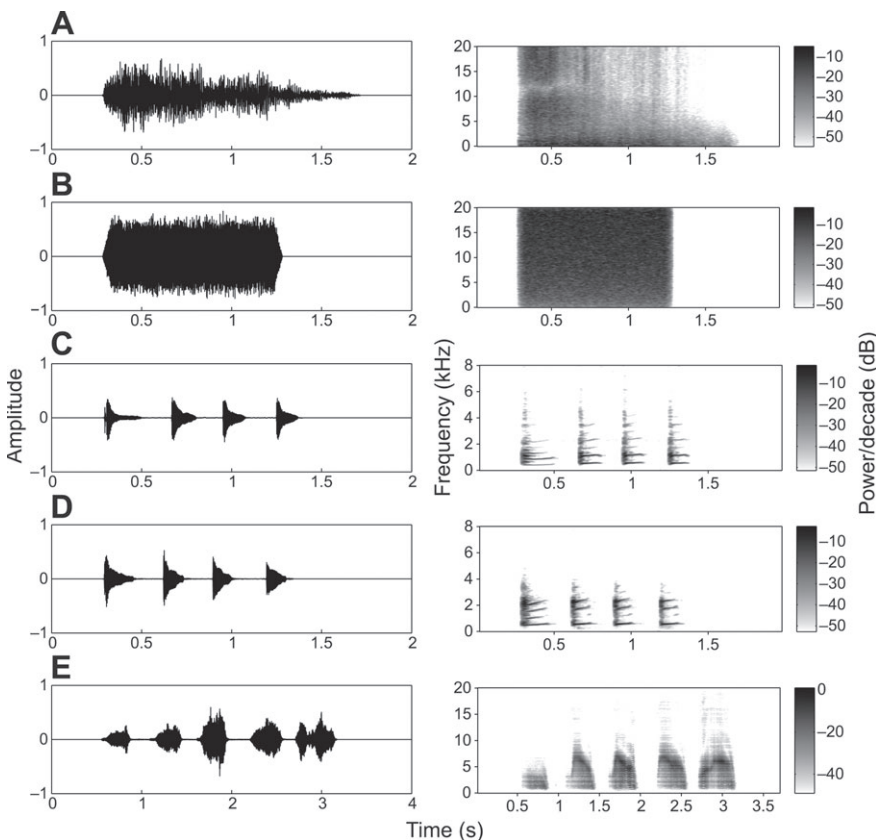


Fig 6. The temporal and spectral structures of the acoustic stimuli used in this study. (A) Thunder, (B) white noise, (C) HSA (high sexual attractiveness) advertisement call, (D) LSA (low sexual attractiveness) advertisement call and (E) screech call. The silence stimulus is not shown.

Software Solutions, Iffezheim, Germany). For computing angular rotation, the snout–tail axis was set as the 0 deg reference. The clockwise turns were identified as right and scored as positive degrees while the counterclockwise turns were identified as left and scored as negative degrees. In cases in which the frog moved less than its snout–tail length, both MA and MD were regarded as zero. The latencies between the onset of each stimulus and the subjects' first reaction were measured offline. In view of the fact that frogs sometimes adjusted their body axis relative to the sound sources more than once during a trial, the total number of active responses by each subject to each stimulus (i.e. turn *in situ* and move away) was counted. The sum of all active responses for each subject to each stimulus constituted the overall behavior score for that subject for each stimulus.

The HSA calls, LSA calls and thunder stimuli were randomly selected from eight exemplars to prevent pseudoreplication as described above. For this reason, in a separate analysis, we statistically evaluated the possibility that behavioral responses differed between the exemplars of the same stimulus types. In addition, we separated the data for each stimulus type on basis of sex to examine the effect of this factor.

Statistical analysis

Because not all data satisfied normality and homogeneity of variance, non-parametric tests were employed using SPSS 20.0 (SPSS Inc., Chicago, IL, USA) in the present study.

A single sample Chi-square test was used to analyze differences between the number of active response patterns and between the number of side orientations within each active response pattern for each stimulus, while a Fisher exact test was used to investigate differences among stimuli. The Friedman test was chosen to examine the differences for TA, MA, MD, latency and behavior scores among stimuli. If the Friedman test was significant, the data were further analyzed for multiple comparisons using the Wilcoxon test. $P < 0.05$ was considered as the level of statistical significance.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

G.F., Y.T. and E.Z. conceived and designed the experiments; F.X. performed the experiments; F.X., G.F., P.Y. and Y.T. analyzed the data; F.X., G.F., S.E.B. and Y.T. interpreted the findings.

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