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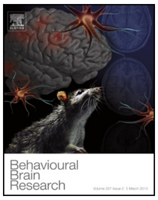

Research report

Right ear advantage for vocal communication in frogs results from both structural asymmetry and attention modulation

Guangzhan Fang[a], Fei Xue[a], Ping Yang[a], Jianguo Cui[a], Steven E. Brauth[b], Yezhong Tang[a,*]

[a] *Chengdu Institute of Biology, Chinese Academy of Sciences, No. 9 Section 4, Renmin Nan Road, Chengdu, Sichuan 610041, PR China*
[b] *Department of Psychology, University of Maryland, College Park, MD 20742, USA*

HIGHLIGHTS

- In female music frogs acoustic stimuli alter left but not right midbrain EEG power.
- Relative left midbrain delta power decreases while alpha and beta power increases.
- The strongest EEG responses are induced by highly sexually attractive male calls.
- Right ear advantage (REA) exists for species-typical stimuli in music frogs.
- REA results from structural asymmetry modulated by attention.

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ABSTRACT

Right-ear/left-hemisphere advantage (REA) in processing species-specific vocalizations has been demonstrated in mammals including humans. Two models for REA are typically proposed, a structural model and an attentional model. These hypotheses were tested in an anuran species, the Emei music frog (*Babina daunchina*) in which females strongly prefer male calls produced from inside mud-retuse burrows (high sexual attractiveness or HSA calls) to those produced in open fields (low sexual attractiveness or LSA calls). Isochronic playbacks were used to control for attention to stimuli presented to either the left or right sides of female subjects while electroencephalogram (EEG) signals were recorded from the left and right midbrain and telencephalon. The results show that relative EEG power in the delta band declined while those of the alpha and beta bands increased with time in the left but not the right midbrain. Since the anuran midbrain receives auditory information derived primarily from the contralateral auditory nerve, these results support the idea that REA occurs in frogs because communication sounds are processed preferentially in the left midbrain. Furthermore, though differences in the dynamic changes of the delta, alpha and beta bands in the left midbrain between acoustic stimuli were not statistically significant, these changes were stronger during the playback of HSA calls toward which females tend to allocate greater attentional resources. These results imply that REA in frogs results from the combined effects of structural asymmetry and attention modulation.

1. Introduction

Specialization of the two hemispheres, i.e. lateralization or asymmetry of brain function, has been described in many vertebrate taxa including fish, frogs, reptiles, birds and mammals [1–3], as a fundamental aspect of nervous system organization [4]. The left hemisphere is specialized to categorize information and responds to features that are invariant and repeated, while the right hemisphere responds to novel events and the expression of intense emotional states such as aggression, escape behavior and fear [5–8]. Functional brain asymmetry may be affected by age, reproductive status and gender [9–11], and can change dynamically even at the level of a few seconds by attention manipulation [12,13].

One phenomenon of asymmetry for either the peripheral or central nervous system is the right-ear advantage (REA) for processing speech sounds in human subjects. REA is usually investigated by means of the dichotic listening (DL) paradigm [14,15]. A putatively homologous REA phenomenon in non-human mammals has been investigated using a head orienting task which involves the processing of species-specific calls in sea lions [16], dogs [17],

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* Corresponding author. Tel.: +86 28 82890799; fax: +86 28 82890288.
E-mail addresses: tangyz@cib.ac.cn, leafmavis@gmail.com (Y. Tang).

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domestic horses [18] and rhesus macaques [19]. To explain the observed hemispheric auditory asymmetry, various models have been proposed, including those based on the temporal and spectral structures of communication sounds [20], on an attentional filter termed the double-filtering-by-frequency model [21] and on different temporal integration windows for each hemisphere termed the asymmetric-sampling-in-time model [22,23]. Multiparametric integration and lateral inhibition at level of the neural network may also be involved in auditory asymmetry, as exemplified by neuronal responses in bats [24]. Most frequently, however, REA has been explained by a structural model and/or an attentional model, corresponding to bottom-up and top-down processing, respectively [25,26].

The structural model emphasizes the "automatic" or "bottom-up" processing biases and posits that REA arises from static asymmetries along the neural pathways connecting the auditory periphery and central auditory structures at the cortical level. The attentional model pinpoints the functional "controlled" or "top-down" factors and posits that aural asymmetries arise from a cognitive or attentional bias directed toward the hemispace contralateral to the engaged cerebral hemisphere. Most theoretical predictions of the structural model for REA have been supported by a body of research [15]. Although the limitations of attentional effects on the REA are still in debate, the manipulation of attentional resources can substantially alter the experimental outcome [27]. Thus, the question of the role of structural asymmetries and attentional variables in bringing about the REA remains a matter of considerable interest.

The electroencephalogram (EEG) allows broad canvassing of brain areas composed of multiple neuronal populations which might be involved in different functions [28]. To evaluate the importance of structural asymmetries and attention modulation in REA processing, we examined the effects of isochronic acoustic stimulation on real time changes in relative EEG power in both the telencephalon and mesencephalon of an anuran species, the Emei music frog (*Babina daunchina*). Previous EEG research indicates that the left hemisphere in *Babina* is specialized for processing species-specific vocalizations [10]. It has been demonstrated anatomically and physiologically in anurans that the right dorsal medullary nucleus (DMN) transfers acoustic information from the right auditory nerve largely to the contralateral superior olivary nucleus (SON) which, in turn, projects to the ipsilateral auditory midbrain, i.e. the torus semicircularis which possesses a well-developed cortical-like layered and uniformly organized structure [29–32]. Thus, a left-hemisphere/right-ear processing advantage for communication sounds in anurans may be mediated by brainstem pathways providing a preferred channel derived from the right ear to the left midbrain and telencephalon. Since both male signaling and female choice are dynamic processes in anurans [33,34], unfolding in real time, REA and its underlying mechanisms would also be expected to estimate by varying dynamically correlated EEG activity in the left hemisphere, especially in the auditory midbrain which is closely associated with the ascending auditory input.

Isochronic playbacks of acoustic stimuli were used in the present study for controlling the subjects' attention to either the left or right side of space. In this way, the subjects were assumed to allocate attentional resources for each hemispace in the same manner for a given stimulus, although they would allocate attentional resources differently depending on the stimulus types. Under these conditions we presumed that (1) no differences in EEG power between the left and right auditory midbrain would be seen when presenting a given stimulus if REA is exclusively attributed to attention; (2) alternatively, processing differences would not be modulated by attention if structural asymmetry is the sole mechanism underlying REA; and (3) dynamic EEG power responses dependent on stimulus types would be observed in the mesencephalon but not the telencephalon because, unlike the condition in amniotes, auditory efferents from the midbrain project broadly throughout the di- and telencephalon in frogs [32].

To test our hypotheses, we recorded multi-channel electrocorticogram (ECoG) signals from female *B. daunchina* in response to silence, a white noise (WN) stimulus and two types of conspecific calls recorded from the same male. Then dynamic differences of EEG power in response to these acoustic stimuli across multiple frequency bands (delta, theta, alpha and beta) in the telencephalon and mesencephalon were evaluated. The possible existence of REA and its mechanisms in frogs were evaluated.

2. Materials and methods

2.1. Animals

Eight female subjects in the reproductive stage were used in this study. Females were used because males normally produce their own advertisement calls in response to stimulus playbacks which would cause EEG artifacts. Subjects were housed in an opaque plastic tank (45 cm × 35 cm and 30 cm deep) containing mud and water. The tank was placed in a room under controlled temperature conditions (23 ± 1 °C) and maintained on a 12:12 light–dark cycle (lights on at 08:00 h). The animals were fed fresh live crickets every three days. Mean masses were 12.0 ± 2.2 g (mean ±SD) and lengths were 4.9 ± 0.2 cm at the time of surgery. All experiments were approved by the Animal Care and Use Committee of Chengdu Institute of Biology.

2.2. Surgery

The surgical procedure used here was described in detail previously [35]. Briefly, sterile surgery was performed under deep anesthesia induced by intraperitoneal pentobarbital sodium (3 mg/100 g). Then, four cortical EEG electrodes, composed of miniature stainless steel screws (φ 0.8 mm), were screwed up into the skull for 2.5 circles to implant at a depth of about 0.8 mm on the left and right sides of the telencephalon and mesencephalon (R1, R2, R3 and R4), and referenced to the electrode above the cerebellum (P, the corresponding electrode pairs were abbreviated as PR1, PR2, PR3 and PR4, respectively) (Fig. 1). R1 and R2 were implanted bilaterally 2.2 mm anterior to the lambda (i.e. the point where skull sutures intersect) and 1.5 mm lateral to the midline, respectively, while R3 and R4 were implanted bilaterally 2.3 mm posterior to the lambda and 1.5 mm lateral to the midline. P was implanted 3.9 mm posterior to the lambda at the midline. One end of a formvar-insulated (except at the two ends) nichrome wire (φ 0.1 mm) served as a ground electrode and was fixed subcutaneously about 5 mm posterior to P.

Each frog was housed singly for two days for recovery before the experiments were performed. After the end of the experiments, all frogs were euthanized by overdose of intraperitoneal pentobarbital sodium and electrode localizations were confirmed by injecting hematoxylin dye through the skull holes in which the electrodes were installed previously.

2.3. Stimulus presentation

B. daunchina males produce advertisement calls during the breeding season both from within nest burrows the male has made and from outside the burrows. The resonant properties of the burrow alter some of the call acoustics, and phonotaxis experiments show that females in the reproductive stage prefer male calls produced from inside burrows [36]. Calls recorded from males within burrows were regarded as highly sexually attractive (HSA) while