Hierarchical auditory perception for species discrimination and individual recognition in the music frog

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Abstract

The ability to discriminate species and recognize individuals is crucial for reproductive success and/or survival in most animals. However, the temporal order and neural localization of these decision-making processes has remained unclear. In this study, event-related potentials (ERPs) were measured in the telencephalon, diencephalon, and mesencephalon of the music frog \textit{Nidirana daunchina}. These ERPs were elicited by calls from 1 group of heterospecifics (recorded from a sympatric anuran species) and 2 groups of conspecifics that differed in their fundamental frequencies. In terms of the polarity and position within the ERP waveform, auditory ERPs generally consist of 4 main components that link to selective attention (N1), stimulus evaluation (P2), identification (N2), and classification (P3). These occur around 100, 200, 250, and 300 ms after stimulus onset, respectively. Our results show that the N1 amplitudes differed significantly between the heterospecific and conspecific calls, but not between the 2 groups of conspecific calls that differed in fundamental frequency. On the other hand, the N2 amplitudes were significantly different between the 2 groups of conspecific calls, suggesting that the music frogs discriminated the species first, followed by individual identification, since N1 and N2 relate to selective attention and stimuli identification, respectively. Moreover, the P2 amplitudes evoked in females were significantly greater than those in males, indicating the existence of sexual dimorphism in auditory discrimination. In addition, both the N1 amplitudes in the left diencephalon and the P2 amplitudes in the left telencephalon were greater than in other brain areas, suggesting left hemispheric dominance in auditory perception. Taken together, our results support the hypothesis that species discrimination and identification of individual characteristics are accomplished sequentially, and that auditory perception exhibits differences between sexes and in spatial dominance.

Keywords: event-related potentials (ERPs), individual identification, music frog, species discrimination, temporal hierarchy

Animals commonly make decisions that are crucial for fitness, including predator avoidance, prey hunting, and conspecific mate searching. One of the greatest challenges that animals are faced with is extracting the relevant properties from vast amounts of sensory information in order to make appropriate decisions (Bidelman and Walker 2019; Green et al. 2020). For example, vocal animals such as birds, anurans, and insects mainly use acoustic signals to transmit diverse information that encodes the signaler's location, size, sex, species, sexual receptivity, and in some cases, individual identity (Gerhardt and Bee 2007; Wells and Schwartz 2007; Naguib et al. 2009; Tobías et al. 2010). Even for vocal species in dense choruses, the capacity to accurately and quickly discriminate between conspecific and heterospecific vocalizations has been demonstrated (Schwartz 1993; Gerhardt 2001). Species discrimination is an important aspect of predator avoidance, prey hunting, and conspecific mate-finding, while conspecific individual recognition is mainly involved in mate and rival identification. To date, relatively few neurophysiological studies have focused on how the brain prioritizes these 2 cognitive processes. Therefore, whether the neural mechanisms underlying species discrimination and individual recognition operate in parallel or sequentially remains an outstanding question.

In most anuran species, vocalization is very important for social interactions and reproductive success (Kelley 2004; Gerhardt and Bee 2007). Species-specific and individually distinct vocalizations serve as complex signals encoding different types of information (Doupe and Kuhl 1999; Feng and Schulp 2007; Yost 2007; Briefer et al. 2010), and function in both mate attraction and territory defense (Tobías et al. 2004; Vignal and Kelley 2007; Bernal et al. 2009; Cui et al. 2010, 2012). In general, different species usually gather in dense breeding choruses to attract mates, creating noisy social environments that may affect communication efficiency (Wells and Schwartz 2007; Bee and Micheyl 2008). For example, rather than calling alone, signaling males with call overlap would presumably benefit from joining a chorus by attracting more females (Gerhardt and Huber 2002; Buxton et al. 2015), reducing the risk of predation by making it harder for predators to locate individuals (Tuttle and Ryan 1982; Wells and Schwartz 2007) or both (Legett et al. 2021). However, overlap of advertisement calls may obscure the fine acoustic features...
of the calls and further affect phonotactic behavior and signal selectivity of females (Marshall et al. 2006). Therefore, a primary challenge for receivers is how to simultaneously detect vocalizations produced by conspecifics and/or heterospecifics in the choruses and respond to them correctly (Brumm and Slabbekoorn 2005; Gerhardt and Bee 2007; Bee 2012; Vélez et al. 2013). Although there is some behavioral evidence for vocal features involved in species discrimination (Feng and Schult 2007), little is known about how animals categorize the vocal signals they receive. Behavioral studies have shown that decision-making for mate selection usually requires several minutes, while eating and fleeing often occur in seconds (Cynx and Nottebohm 1992; Schwartz et al. 2004; Marshall et al. 2006). Although the different response latencies could result from different behavioral motivations evoked by heterospecific and conspecific signals, the difference in response time also implies that individual recognition based on acoustic signals may occur after species discrimination based on acoustic and/or other modal signals in anurans. In the current study, we tested for priorities of neural signal processing of conspecific and heterospecific signals in auditory perception.

Many anuran species advertise vocally together in wetlands or ponds during the breeding season. Among such species, the Emei music frog (Nidirana daunchina) and the Asian spiny frog (Quasipaa boulengeri) often occupy the same pond, have overlapping breeding seasons, and call side by side (Ye et al. 1993; Fei et al. 2009; Cui et al. 2010; Qing et al. 2012; Fang et al. 2014a). Male music frogs produce advertisement calls either from inside underground nest burrows or from outside burrows (Cui et al. 2012). Males of both species produce advertisement calls consisting of trains of stereotyped notes to attract conspecific females and deter rivals. Thus, overlapping conspecific and/or heterospecific calls cannot be avoided in these dense choruses, which may obscure the auditory perception of the fine temporal components and vocal structures (Schwartz 1987). The reproductive success of the music frog requires that both male and female music frogs can discriminate species and identify conspecific individuals on the basis of advertisement calls. Moreover, our previous study has found that the music frog can divide acoustic signals into general categories prior to classifying them further into subtypes (Fang et al. 2015). For these reasons, the Emei music frog was used as an animal model to test the hypothesis that species and individual characteristics are processed sequentially in the auditory system.

Event-related potentials (ERPs) are time-locked responses of brain activities evoked by a given event, whose amplitudes and latencies can reflect the efficiency and time course of neural processing (Näätänen and Picton 1987). In terms of their polarity and position within the ERP waveform, 4 components of auditory ERPs are commonly labeled as N1, P2, N2, and P3. These may link to selective attention, stimulus evaluation, identification, and classification, and occur around 100, 200, 250, and 300 ms post-stimulus, respectively. Specifically, greater N1 amplitudes can be evoked by attended sounds compared with unattended ones, suggesting that the amplitude of N1 can reflect selective attention such that the brain selectively attenuates sensory input to the unattended sounds from further processing (Hillyard et al. 1973). Although the functional significance of P2 is poorly understood, it has been suggested to represent stimulus evaluation and attention-modulated stimulus classification processes (Crowley and Colrain 2004; Wang et al. 2019). N2 is typically evoked before the motor response, suggesting its link to the cognitive processes of stimulus identification and distinction (Hoffman 1990). An unexpected/novel stimulus interspersed among uniform/standard stimuli can elicit a high P3, also known as “novelty P3”, which reflects a classification process (Cycowicz and Friedman 1997). Furthermore, in order to explore the direct relationship between ERP components and physical properties of the eliciting stimulus, ERP components can be classified as exogenous or endogenous according to whether they are directly influenced by external or internal factors (Muller-Gass and Campbell 2002; Luck 2005). The former, which includes N1 and P2, represents cognitive processing at the sensation level and are primarily affected by the physical parameters of the stimulus. On the other hand, the latter, which includes N2 and P3, represents cognitive processing at the perception level and are primarily affected by the psychological relevance of the stimulus. Moreover, human-like auditory ERP components found in various taxa such as primates (Arthur and Starr 1984), mammals (Woods et al. 1986; Ehlers et al. 1994), and anurans (Fang et al. 2015; Fan et al. 2018, 2019; Yang et al. 2018; Shen et al. 2020) may indicate similar brain functions across these taxa, because important neuroanatomical features have been conserved during vertebrate brain evolution (Finlay et al. 2001; Northcutt 2002).

Due to their excellent temporal resolution, ERPs were used in the present study to assess when and in which brain regions the discrimination of species and identification of individuals occurs. To this end, the present study measured the amplitudes and latencies of ERP components in the left and right telencephalon, diencephalon, and mesencephalon in response to 3 groups of auditory stimuli (heterospecific advertisement calls of the Asian spiny frog, and 2 groups of randomly assigned conspecific advertisement calls acquired from conspecific individuals with different fundamental frequencies) in order to provide information concerning the priority of neural signal processing for conspecific and heterospecific signals. We predicted that (1) conspecific advertisement calls would elicit a larger N1 compared with the heterospecific calls because the former can attract more attention resources of the receivers; (2) P2 or N2 amplitudes would differ significantly between the 2 groups of conspecific calls because these components relate to signal evaluation and identification; (3) heterospecific calls would evoke a larger P3 than the conspecific ones, as the receivers would classify the conspecific calls into 1 category and perceive the heterospecific calls as novel; and (4) ERP components might exhibit both sexual dimorphism and left hemispheric dominance since these 2 attributes have been noted in auditory perception in anurans (Fan et al. 2018; Shen et al. 2020).

Materials and Methods

Animals

The experiment was conducted on 16 adult N. daunchina frogs of both sexes (8 females and 8 males) captured from the Emei mountain area of Sichuan, China. The frogs were separated by sex and housed in different plastic tanks (45 × 35 cm2 and 30 cm deep) with mud and water. The tanks were held at a constant temperature (23 ± 1°C) and a 12:12 light–dark cycle (lights on at 08:00). The frogs were fed fresh live crickets every 3 days. At the time of surgery, the females were 12.42 ± 2.84 g in body mass (mean ± s.d.) and 5.03 ± 0.39 cm...
in body length; the males were $8.86 \pm 1.43$ g in body mass and $4.65 \pm 0.24$ cm in body length.

**Surgery**
All experiments were conducted during the reproductive season of this species. Surgical procedures are described in detail in our previous studies (Fan et al. 2018; Shen et al. 2020). Before the surgery, the frogs were deeply anesthetized via a water bath in a 0.2% tricaine methanesulfonate (MS-222) solution. Six cortical electroencephalogram (EEG) recording electrodes consisting of miniature stainless-steel screws ($\varphi$ 0.8 mm) were implanted in the skull, above both the left and right sides of the telencephalon, diencephalon, and mesencephalon. A reference electrode was implanted above the cerebellum (Figure 1) and served as the reference point against which the recording electrode of interest was measured. All electrode leads were formvar-insulated nichrome wires that were wound together around a pencil to form a loose spring for best suspension. Each subject was housed individually for a one-week recovery period before performing further experiments. After all experiments were completed, the subjects were euthanized by an overdose of MS-222 solution. Hematoxylin dye was then injected into the skull holes in which the electrodes were installed. This was done to determine the electrode localizations in the predetermined brain area, in order to verify that recordings were taken from appropriate brain regions (Fang et al. 2012).

**Recording conditions**
An opaque plastic tank (80 × 60 cm$^2$; 55 cm deep) paved with mud and water was placed in a soundproof and electro-magnetically shielded chamber (background noise 23.0 ± 1.7 dB; re 20 µPa, C-weighting, fast response; Aihua, AWA6291; Hangzhou, China). An infrared camera with a motion detector was mounted centrally, approximately 1 m above the tank to monitor the frogs’ behavior. Electrophysiological signals were recorded with a signal acquisition system (OmniPlex 64-D, Plexon, USA). The band pass filter was set to 0.05–200 Hz for filtering EEG signals with a sampling rate of 1,000 Hz.

**Stimulus and procedure**
Since pseudoreplication may affect the results of statistical analyses in ecological, animal behavior, and neuroscience studies (Kroodsma et al. 2001; Freeberg and Lucas 2009; Schank and Koehnle 2009; Lazic 2010), we controlled for these possible effects by using multiple stimulus exemplars. Specifically, we randomly selected 8 conspecific advertisement calls containing 4 notes recorded from 8 conspecific individuals inside their underground nest burrows. Four heterospecific advertisement calls, consisting of 6 notes, were acquired from 4 heterospecific individuals of the sympatric species, the Asian spiny frog. Both conspecific and heterospecific calls possessed similar durations, and their temporal and frequency parameters were close to the average values of the corresponding populations. These calls were assigned into 4 stimulus sets, each containing 2 randomly selected conspecific calls and 1 randomly selected heterospecific call (Figure 2). Importantly, fundamental frequency and correlated spectral properties are the most individually distinct call properties and contribute the most toward assigning calls to the correct individuals for most frogs (Gerhardt and Bee 2007; Fang et al. 2019), including the music frog (Chen et al. 2011). Hence, we analyzed and compared the fundamental frequencies of the 2 conspecific calls in each stimulus set. Next, in order to statistically compare the difference in neural responses to different conspecific calls, the 8 conspecific calls were further divided into 2 groups: one contained 4 conspecific calls with relatively higher fundamental frequencies (each call from each stimulus set) and the other contained 4 conspecific calls with relatively lower fundamental frequencies. Each stimulus set was played back to 4 subjects (2 males and 2 females), and that all subjects never heard the stimuli before.

The stimuli were presented through 2 portable field speakers (frequency response: 100–12,000 Hz; SME-AFS, Saul Mineroff Electronics, NY, USA) at 65 dB SPL (re 20 µPa, C-weighting, fast response; Aihua, AWA6291; Hangzhou, China) measured at the center of the experimental tank. Before the experiments, 1000 Hz tones were used to calibrate the peak output intensity of each speaker to 70 dB SPL (measured 1 m from the speaker). Because the influence of the target stimulus probability on P3 amplitude would wane considerably under longer inter-stimulus intervals (ISIs) (Polich 1990; Gonsalvez and Polich 2002), the ISI was set to 1.5 s, although the mean natural inter-call interval of this species is 3.3 s (Fang et al. 2014a). For each awake and freely moving subject, a total of 300 stimulus presentations with each stimulus repeatedly presented 100 times were generated in a random order within 3 trial blocks. Randomization was constrained such that more than 3 stimuli from 1 acoustic category were not presented successively. The session lasted about 25 min, with 5 min breaks between blocks to prevent the subjects from becoming fatigued (Deveney and Pizzagalli 2008).

**Acoustic parameter analysis for stimuli**
To compare differences in the acoustic features of the stimuli, we measured 19 parameters for each stimulus: call duration, duration of each of the first 4 notes, inter-note intervals among the first 4 notes, fundamental frequency for each of the first 4 notes, differences in fundamental frequency among the first 4 notes, and number of harmonics in each of the first 4 notes. The 8 temporal parameters were measured from the waveforms of the stimuli using Adobe Audition 3.0 software (San Jose, CA, USA), and that thresholding of the vocalizations was set at -48 dB. The 11 frequency parameters were measured using Praat software (version 6.1.13) from the spectrograms of the stimuli. All of the abovementioned acoustic
parameters for all exemplars (conspecific and heterospecific calls) were analyzed with hierarchical cluster analysis and multidimensional scaling analysis with Euclidean distance as the metric. The following default criteria were used: s-stress convergence set at 0.001, minimum s-stress value set at 0.005, and maximum iterations set at 30.

ERP analysis
To extract ERP components, raw EEG recordings were filtered offline using a bandpass filter of 0.25–25 Hz and a notch filter to eliminate possible interference at 50 Hz before averaging the stimulus-locked EEG periods. The EEG signals were divided into periods of 700 ms in duration, including a 200 ms pre-stimulus baseline. All single EEG trials were inspected visually and trials with muscle artifacts and electrode drifts were removed from all further analysis. The accepted trials (roughly 80 out of 100 trials for each stimulus group and each animal) were averaged according to stimulus group and brain area.

For each ERP component, the peak could be found in the grand average waveforms for each brain area and each stimulus. The median was then calculated regardless of brain area or stimulus. Consequently, the ERP component N1 was defined as the mean amplitude during intervals of 40–80 ms, P2 for 160–200 ms, N2 for 210–250 ms, and P3 for 285–355 ms after the stimulus onset (Ostroff et al. 2003; Yago et al. 2003; McDonald et al. 2005; Patel and Azzam 2005). The latency of each component was determined by the “50% area latency measure”, that is, measuring the area under the curve within the time windows and finding the time point that divided this area into equal halves (Luck 2005). The amplitudes and latencies acquired from the original waveforms were subjected to further statistical analyses for each ERP component.

Statistical analyses
The normality of the distribution and homogeneity of variance for amplitude or latency of each ERP component were estimated with the Shapiro–Wilk W test and Levene’s test, respectively. For the waveforms, amplitudes and latencies of N1, P2, N2, and P3 were statistically analyzed using a 4-way repeated measures ANOVA with the variables of “stimulus set” (the 4 stimulus sets), “sex” (female/male), “acoustic stimulus” (1 group of heterospecific calls and 2 groups of conspecific calls), and “brain area” (the 6 brain regions). There was no significant main effect of “stimulus set” for any of these ANOVAs, consistent with the idea that the 4 stimulus sets were not significantly different at eliciting responses from the subjects. Thus, each dataset was pooled regardless of “stimulus set” and statistically analyzed using a 3-way repeated measures ANOVA with the other 3 factors. Both main effects and interactions were examined. When ANOVAs were significant, the data were further analyzed for multiple comparisons using the least significant difference (LSD) test. Greenhouse–Geisser epsilon (ε) values were employed when the Greenhouse–Geisser correction was necessary. Effect size was determined with partial $\eta^2$ (partial $\eta^2 = 0.20$ is set as a small, 0.50 a medium, and 0.80 a large effect size) (Cohen 1992). SPSS software (release 21.0) was utilized for the statistical analysis; $P < 0.05$ was set as the significance level, while $P$ values >0.05 and <0.1 were deemed marginally significant (Utts and Heckard 2006).

Results
In the grand average waveforms, N1, P2, N2, and P3 can be seen clearly for each brain area and each acoustic stimulus (Figure 3). For amplitude, there were significant differences
among acoustic stimuli, brain areas, or sexes. However, none of these differed for latencies.

Acoustic parameters of stimulating calls
As expected, the hierarchical cluster analysis revealed 2 clusters for the 3 groups of stimuli: the heterospecific calls formed the first cluster, while the conspecific calls formed the second (Figure 4A). Similarly, the multidimensional scaling analysis mapped most of the variance among the acoustic parameters to 2 dimensions (Figure 4B). The Euclidean distance in dimension 1 between the heterospecific and conspecific calls was greater than 2.0; however, the distance between the 2 groups of conspecific calls was indistinguishable (Figure 4B).

Amplitude and latency of the N1 component related to selective attention
For N1 amplitude, the main effects were significant for “acoustic stimulus” ($F_{2,30} = 9.571$, partial $\eta^2 = 0.406$, $P = 0.001$) and “brain area” ($F_{5,75} = 2.571$, partial $\eta^2 = 0.155$, $P = 0.034$), but not for “sex” ($F_{1,14} = 0.003$, partial $\eta^2 < 0.001$, $P = 0.961$). The amplitudes elicited by the conspecific calls were significantly larger than those evoked by the heterospecific calls ($t = 3.983$ and $P = 0.001$ for the conspecific calls with relatively lower fundamental frequencies; $t = 2.830$ and $P = 0.013$ for the conspecific calls with relatively higher fundamental frequencies, Figure 5A). The N1 latency in the left diencephalon was significantly higher than the latencies in the right diencephalon, right mesencephalon, and both sides of the telencephalon (all $t \geq 2.404$ and all $P \leq 0.038$, Figure 5A). The N1 latency did not show a significant main effect for any of the factors (all $P \geq 0.314$ for “acoustic stimulus”, “brain area”, and “sex”).

Amplitude and latency of the P2 component related to stimulus evaluation
For P2 amplitude, the main effects were significant for “sex” ($F_{1,14} = 9.894$, partial $\eta^2 = 0.414$, $P = 0.007$) and “brain area” ($F_{5,70} = 5.183$, partial $\eta^2 = 0.270$, $P < 0.001$), but not for “acoustic stimulus” ($F_{2,30} = 0.402$, partial $\eta^2 = 0.028$, $P = 0.673$). The P2 amplitude evoked in females was significantly higher than the amplitude evoked in males ($t = 3.150$ and $P = 0.007$). The P2 amplitudes in both sides of the telencephalon and diencephalon were significantly higher than those evoked in the right mesencephalon, while the amplitude in the left telencephalon was significantly higher than those evoked in both sides of the diencephalon and the left mesencephalon (all $t \geq 2.169$ and all $P \leq 0.047$, Figure 5B). The P2 latency did not show a significant main effect for any of the factors (all $P \geq 0.125$ for “acoustic stimulus”, “brain area”, and “sex”).
Amplitude and latency of the N2 component related to stimulus identification

For N2 amplitude, the main effect was significant for “acoustic stimulus” (F(5,70) = 6.444, partial η² = 0.315, P = 0.005), but not for “sex” (F(1,14) = 2.688, partial η² = 0.161, P = 0.123) or “brain area” (F(5,70) = 0.750, partial η² = 0.051, P = 0.589). The N2 amplitudes elicited by the heterospecific calls (t = 3.012, P = 0.009) and the conspecific calls with relatively lower fundamental frequencies (t = 2.175, P = 0.047) were significantly higher than those evoked by the conspecific calls with relatively higher fundamental frequencies. The N2 amplitude elicited by the heterospecific calls was marginally significantly higher than that elicited by the conspecific calls with relatively lower fundamental frequencies (t = 2.175, P = 0.047). The N2 latency was not significant for the main effect of any factor (all P ≥ 0.104 for “acoustic stimulus”, “brain area”, and “sex”).

Amplitude and latency of the P3 component related to stimulus classification

For P3 amplitude, the main effect was significant for “acoustic stimulus” (F(5,70) = 4.764, partial η² = 0.254, ε = 0.728, P = 0.029), but not for “sex” (F(1,14) = 0.711, partial η² = 0.048, P = 0.413) or “brain area” (F(5,70) = 0.800, partial η² = 0.054, ε = 0.506, P = 0.483). The P3 amplitude in response to the heterospecific calls was significantly higher than those to the conspecific calls (t = 2.660 and P = 0.019 for the conspecific calls with relatively lower fundamental frequencies; t = 2.227 and P = 0.043 for the conspecific calls with relatively higher fundamental frequencies, Figure 5E). The P3 latency did not show a significant main effect for any of the factors (all P ≥ 0.126 for “acoustic stimulus”, “brain area”, and “sex”).

Discussion

Species discrimination first, then individual identification

Previous studies on acoustic parameter analysis have shown that differences in the acoustic characteristics of calls were greater between species than among individuals within a species (Brooks and Falls 1975; Bee and Gerhardt 2001). Hence, neural systems might divide signals into general categories prior to classifying them further into subtypes (De Lucia et al. 2010). Consequently, sequential model of mate choice supposes that animals might engage in a sequential process for mate choice, in which individuals must first choose the right species before choosing the highest quality conspecific mate (Mendelson and Shaw 2012). It seems clear that different components of signals can indicate (or correlate with) different axes of mate quality, one of which might be compatibility in an interspecific context (Mendelson and Shaw 2012). In view of fitness consequences and multidimensional nature of mate choice, the sequential model could be further described as signals indicating compatibility are processed, perceived, and responded to before signals that indicate some other axis of quality (Mendelson and Shaw 2012). Consistent with this hypothesis, the N1 amplitudes elicited by the advertisement calls of the music frogs were significantly greater than those evoked by the calls of the Asian spiny frogs. The earliest ERP component, N1, sensitive to the onset parameters of the stimuli (Biermann and Heil 2000) is known as “exogenous” or “stimulus bound”, and represents cognitive processing at the sensation level (Muller-Gass and Campbell 2002; Luck 2005). During the breeding season, anurans must focus constant attention on conspecific advertisement calls that encode information associated with potential mates or rivals, as well as information related to danger (Kelley 2004). Male music frogs produce advertisement calls either from inside underground nest burrows or from outside burrows (Cui et al. 2012). Behavioral experiments revealed that females prefer the former and males are more likely to compete against the former compared with the latter (Cui et al. 2012; Fang et al. 2014a). Taken together, these findings are consistent with the idea that selective attention may be involved in anuran auditory perception (Greenfield and Rand 2000; Krauzlis et al. 2018). The Asian spiny frog calls could indicate that there are no predators around, thus this stimulus could act as an index
Figure 5. Means and standard deviations for the N1 (A), P2 for females (B), P2 for males (C), N2 (D) and P3 (E) amplitudes evoked by each acoustic stimulus in each brain region (n = 16). Note that the amplitudes except for P2 were averaged regardless of sex for a better demonstration because significant sex difference only exhibited for P2. Abbreviations: LT and RT, left and right telencephalon; LD and RD, left and right diencephalon; LM and RM, left and right mesencephalon; HC, heterospecific calls; CCL, conspecific calls with relatively lower fundamental frequencies; and CCH, conspecific calls with relatively higher fundamental frequencies. *0.05 ≤ P < 0.1; *P < 0.05; **P < 0.001.
of safe surroundings, albeit with no contribution to reproductive success in the music frog. Hence, individuals might use selective attention mechanisms to focus on perceiving conspecific calls that might contain more compatible information compared with the heterospecific ones. Indeed, the greater “N1 effect of selective attention” (Hillyard et al. 1973; Fang et al. 2015) was exhibited for the conspecific calls compared with the heterospecific ones, suggesting compatibility indicators in the calls might be processed first in a sequence (Mendelson and Shaw 2012). Accordingly, the neural processing for species discrimination at the sensation level was completed within 100 ms after stimulus onset. This finding is in agreement with a previous study on humans, in which the discrimination of auditory objects was found to occur at 70 ms, while task-related effects occurred 100 ms after stimulus onset (Murray et al. 2006). Furthermore, in response to the heterospecific calls and the conspecific calls with relatively lower fundamental frequencies, the N2 amplitudes are significantly higher than those evoked by the conspecific calls with relatively higher fundamental frequencies. The N2 amplitudes evoked by the heterospecific calls are marginally significantly higher than those evoked by the conspecific calls with relatively lower fundamental frequencies. Fundamental frequency and the correlated spectral properties are the most individually distinct call properties, and have been shown to contribute most toward assigning calls to the correct individuals for most frogs (Gerhardt and Bee 2007; Chen et al. 2011; Fang et al. 2019). Moreover, N2 is linked to the cognitive processes of stimulus identification and distinction (Hoffman 1990). The individual recognition in music frogs was considered to be completed around 200 ms, hence species and individual information appear to be decoded in order, as reflected by ERP components in the tested music frogs, which provides strong support for sequential model of mate choice (Mendelson and Shaw 2012). Nevertheless, future studies are needed for a comprehensive understanding of the ability to discriminate species and recognize individuals at the behavioral level using behavioral experiments such as binary playback tests.

Although vocalization discrimination in humans may be modulated by the semantic content of stimuli (Charest et al. 2009) and the attention of participants to the speakers’ voices (Levy et al. 2001, 2003), humans still discriminate acoustic cues with a temporal hierarchy: 1) human-produced versus natural sounds are discriminated first at 70–119 ms, followed by 2) discrimination of non-human animal sounds versus human non-verbal vocalizations at 169–219 ms, and 3) continued discrimination of subtypes of anthropogenic sounds as well as speech at 291–357 ms (Murray and Spierer 2009; De Lucia et al. 2010; Spierer et al. 2011). Since the time windows for species discrimination and individual identification in the music frog are similar to those for sound discriminations in humans, it is possible that temporal hierarchical mechanisms for auditory perception in classifying various sounds are similar in different species.

The P3 amplitude evoked by the heterospecific calls was significantly greater than those evoked by the conspecific calls, consistent with the idea that within the first 300 ms, individuals had already categorized the conspecific calls into 1 category and perceived the heterospecific calls as novel at the perception level because of the endogenous attribute of P3. The typical P3 component is most strongly elicited using oddball paradigms in which subjects are exposed to small portions of unexpected/novel stimuli interspersed between major portions of uniform/standard stimuli (Novak et al. 1992; Friedman et al. 2001). In the present study, the equiprobability paradigm could produce an oddball-like paradigm in which the 2 groups of the conspecific calls could serve as the major stimulation (66.7% probability) while the heterospecific calls served as a minor novelty (33.3% probability). Thus, a larger P3 could be evoked by the heterospecific calls because the animals categorized the 2 groups of conspecific calls into 1 category, as expected.

Auditory perception exhibits a sex difference

Sexual dimorphism in auditory perception exists in many taxa including vocal animals (Del Negro and Edeline 2001; Fan et al. 2018; Yang et al. 2018), which can be reflected by the ERP components such as N2 and P2 related to the process of signal evaluation and identification (Hoffman 1990; Crowley and Colrain 2004; Wang et al. 2019). Consistent with this, the present results showed that the P2 amplitudes evoked by the acoustic stimuli in females were significantly higher than those in males, suggesting that females likely devoted more brain resources to auditory perception than males. Sexual selection theory predicts that females should be more choosy in mate choice than males, while males are more permissive than females (Bernal et al. 2007; Hoke et al. 2008). For example, when heterospecific advertisement calls of 14 species were broadcasted to túngara frogs (Physalaemus pustulosus), females were more likely to show phonotaxis to calls of closely related species and ancestors, while males compete vocally in response to the calls of most species (Bernal et al. 2007). Furthermore, signal detection theory also demonstrated that the cost of missed identification of conspecific solicitation signals from heterospecific ones would be greater in females than males, while the cost of not responding to potential sexual cues would be greater in males than females (Green and Swets 1966; Wiley 2006). Consequently, compared with males, females must make more effort to discriminate the subtle differences between acoustic signals before making a decision, that is, requiring more brain resources for auditory perception. Hence, sexual dimorphism in auditory processing may reflect differences in the requirement for neural processing of the sex-specific aspect of acoustic signals (Hoke et al. 2010). Nevertheless, psychological responses to acoustic signals should be tested using behavioral experiments in future studies.

Auditory perception exhibits left forebrain dominance

Both N1 amplitudes in the left diencephalon and P2 amplitudes in the left telencephalon evoked by the acoustic stimuli were the largest compared among the tested brain areas, indicating that left forebrain dominance exists for auditory perception. These results are generally consistent with other studies on N1 and P2, which have also suggested that the left forebrain may play a crucial role in auditory perception (Fan et al. 2018). Previous studies have demonstrated that complex signals such as conspecific advertisement calls can induce large neuronal responses and immediate early gene (IEG) expression in multiple forebrain structures (striatum and medial pallium) (Mangiamele and Burmeister
and lesions of the striatum and thalamic nuclei may disrupt vocal recognition (Endepols et al. 2003). Accordingly, we have previously demonstrated that auditory signals are preferentially processed in the left hemisphere in *N. daunchina* (Fang et al. 2014b; Yue et al. 2017; Yang et al. 2018; Fan et al. 2019) and *Xenopus laevis* (Fan et al. 2018). Taken together with the present results, the accumulating evidence points to a crucial role for the left forebrain in auditory perception in anurans. Consequently, more forebrain resources appear to be involved in higher level cognition functions such as hierarchical auditory perception for species discrimination and individual identification.

In summary, we found that the neural processing for species discrimination at the sensation level was accomplished within 100 ms, while individual identification was completed around 200 ms. Hence, species discrimination and identification of individual characteristics occur sequentially in the music frog. Moreover, the amplitudes of ERPs elicited in females and in the left forebrain were greater than those in males and in the other brain areas, respectively, suggesting sexual dimorphism and left forebrain dominance in auditory perception in this species.

**Ethical statement**

All studies were conducted under approval of the Animal Care and Use Committee of Chengdu Institute of Biology, Chinese Academy of Sciences (permit number: 20191203).

**Availability of data and materials**

The dataset generated and analyzed during the current study are available in the GitHub repository: https://github.com/myleafmavis/data_analysed.git.

**Authors’ contributions**

G.F. conceived the study. Y.F., Y.T., and G.F. designed the research. K.F. and D.S. performed the animal surgery. K.F., R.S., and J.Y. participated in data collection. Y.F. and R.S. carried out data analysis. Y.F. drafted the manuscript. Y.T. and G.F. revised the manuscript. All authors read and approved the final manuscript.

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**Conflict of interest**

The authors declare that they have no competing interests.

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