



## Perception and Recognition of Vocalization in Anuran Mate Choice

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**Abstract** Vocal communications in frogs and toads have been highly diversified and become a hot topic in the fields of herpetology, ecology, and behavioral neuroscience. The present short review summarized several interesting phenomena of vocal communication found mainly in anurans that might contribute to the individual identification of mates or rivals, including call matching, aggressive signaling, acoustic complexity, signal exaggeration, the first note effect and left hemisphere dominance. Investigations on the perception and recognition of vocal communications will facilitate our comprehension of the adaptive mechanisms and evolutionary paths of anuran signaling systems. We proposed here that comparative studies on acoustic signal structures, codes of sender status, and auditory neural responses based on phylogenetic relationships across species can highlight further the evolutionary trajectory in anurans.

**Keywords** anuran, adaptive mechanism, evolution, phonotaxis, vocal communication

Mate choice can generate a sexual selection and then genetically isolate species from one another, which begins generally with signal detection, and then moves to evaluate information (perception and recognition) and acts on it (Ryan *et al.*, 2009). Acoustic signal detection is usually dependent on the sender side with increasing its signal contrast out of the background and the receiver side with its enhanced specific sensibility to signals, which is involved mostly in the peripheral vocal and auditory systems. Perception and recognition occurred in the central nervous systems, are two intermingled processes before decision-making. Therefore, many vocal traits and auditory characters are proposed to evolve for the process of perception and recognition in anurans (Ryan, 2013; Ryan and Cummings, 2013), which would promote the individual identification of mates or rivals and decoding their vocalizations. Although many animals produce acoustic signals to express stereotypically the biological significance, three animal taxa are studied widely in their vocalization and communication, including insects, anurans, and birds (Garcia and Favaro, 2017). Most previous studies of anuran vocalizations have focused behaviorally on mate choice under the theoretic frame of sexual selection, and increased researches have probed the auditory perception and recognition in anurans during the past two decades (Ryan, 2009). It has been established that anurans' calling and responding to calls are attributed predominantly to their instincts (Dawson and Ryan, 2009), in contrast to some species of songbirds whose song patterns are resulted largely from vocal learning during the specific period before breeding (Yanagihara and Yazaki-Sugiyama, 2016; Mason *et al.*, 2017). Therefore, the investigation of anuran vocalization might facilitate our understanding of

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evolutions of vocal communications in vertebrates.

Perception and recognition studies have advanced greatly in the last three decades in human subjects and a few typical animals, including primates and rodents, with a large body of investigations focusing on auditory processing (Bregman, 2017). However, primates and rodents do not use vocal signaling as a predominant way for communication in mate choices (Keddy-Hector, 1992; Johnston, 2003).

## 1. Call Matching

Coevolution between signal senders (usual males) and receivers (both males and females) might occur under the selection pressure of improving the efficiency of animal communication (McClelland *et al.*, 1998; Ryan, 1988; Cui *et al.*, 2016a), e.g. acoustic characteristics in calls are matched evolutionarily by the auditory sensitivity in the receiver side. This phenomenon was first reported in the cricket frog (*Acris crepitans*). Two populations about 70 km apart with each population possessing its specific dominant frequency (DF) in calls and sensitive frequency (SF) in the receiver's auditory system showed that DF and SF were significantly closer within the population than between populations (Ryan, 1988). In general, variations in call frequencies were reversely correlated with the signaler's body sizes while the auditory sensitivity was largely influenced by the reproductive states of females (Wang *et al.*, 2012; Zhang *et al.*, 2012). The acoustic matches were also investigated in insects (Bush and Schul, 2006), lizards (Brittan-Powell *et al.*, 2010; Chen *et al.*, 2016; Yu *et al.*, 2011) and birds (Groth, 1993). Most anuran species studied to date present similar matching patterns, with a few exceptional samples of unmatching ones (Zhao *et al.*, 2017; Zhu *et al.*, 2017).

The acoustic match could be found not only in the frequency domains but also in the temporal sequence of signals. For instance, the mormyrid fish (*Pollimyrus adspersus*) showed an auditory specialization for weak sound detection of conspecific signals from the noisy water environment. A mormyrid fish call consisted of click chains with inter-click-interval (ICI) of 18 ms and its auditory system could follow these rhythms precisely while no dependable response was found to stimulations with shorter or longer ICI (Crawford, 1997). Neurons in the midbrain (nucleus *torus semicircularis*) of two frog species displayed the responsive selectivity for temporal features such as pulse rate, pulse duration, number of pulses, pulse rise time/fall time, train duration, and two types of pulse-amplitude-modulation (Penna *et al.*, 1997, 2001). In leopard frogs (*Rana pipiens*), four categories of responsively temporal patterns were recorded from the midbrain neurons: all pass, long-duration pass, band duration pass, and short duration pass (Feng *et al.*, 1990; Gooler and Feng, 1992). An extreme example of the acoustic match was found in

tree frogs (*H. regilla*) in which auditory neurons in the midbrain fired exclusively in response to the stimulus with nine pulses which the conspecific calls comprised (Edwards *et al.*, 2002). It is most likely that there was an innate "counter", probably a simple neuron network, in the brains of both signal sender and receiver to synchronize their signaling temporality (Edwards *et al.*, 2008; Rose *et al.*, 2011).

This acoustic match may point to an evolutionary mechanism for improving animal communication. Interestingly for some anuran species, the sexual traits or acoustic features in the advertisement call which are favored by females have not evolved in conspecific males, suggesting that the female's bias for a trait originates before the male's capability of generating it (Ryan *et al.*, 1990). Similar phenomena are also found in the visual systems of fishes and other animals (Ryan, 1998). Therefore, the "sensory exploitation" hypothesis was proposed to explain the signal origination in those species: males who evolve traits that exploit those preexisting preferences are favored by sexual selection (Ryan *et al.*, 1990; Ryan, 1998; Feinberg *et al.*, 2018). Some recent studies indicated that "old" species seemed to have completed the "match process" while some "new" species or those exploiting newly leks are still in the matching process, showing partially acoustic matching (Zhao *et al.*, 2017; Zhu *et al.*, 2017; Yang *et al.*, 2019).

In his book *On Aggression*, Lorenz proposed that signaling systems might originate from an "occasional" action/response which "happens" to convey information between individuals and then could be the subject of natural or sexual selection (Lorenz, 1963). The efficiency and accuracy of communication could be improved eventually through a process called ritualization, indeed a "natural practice" with rigid, exaggerated, and repetitive patterns in actions. However, there is an ongoing argument on how a given signaling process, a complicated neural episode, has been imprinted in DNA sequences that are linearly aligned (Robinson and Barron, 2017). If the evolution of the communication system abides by the Darwinian procedure, there must be mutations of, at least, two genes or variations in a population with one for signal production in the sender (e.g. male) and another for signal perception in the receiver (e.g. female), respectively, which have to occur in the same species within the same generation living at the same territory.

## 2. Aggressive vs. Advertisement Signaling

Many male frogs defend their territories against conspecifics, often by emitting vocally aggressive signals. Aggressive and advertisement calls usually consist of similar dominant frequencies, but are different in temporal structures. For example, advertisement calls of some species including the spring peeper (*Pseudacris crucifer*) are longer tone-like sounds

while their aggressive calls contain a series of shorter pulses (Wells, 1980). Other species show a reverse pattern, e.g. males produce pulsed advertisement calls with distinctly different pulse rates, but tone-like, slightly frequency-modulated, aggressive calls (Owen, 2003; Owen and Gordon, 2005). These calls sometimes grade into each other as a male makes the transition from aggressive to advertisement calling (Wells and Schwartz, 2007). Males of *Fejervarya nicobariensis* utter multiple-note advertisement calls with 1 to 6 click notes, but when they are calling nearby, males produce up to 25 notes of aggressive calls (Jehle and Arak 1998).

It is likely that aggressive calls are unable to repulse the rivals from closely neighboring sites but can change their calling strategies. Then, high plasticity of aggressive signaling can be expected (Marshall *et al.*, 2003). Furthermore, aggressive calls are produced at the expense of advertisement calls if a male's calling effort is near its upper limit. A positive correlation between the amplitude of the advertisement calls of a male's nearest neighbor and the stimulus amplitude at which the male first produces aggressive calls is established in the spring peepers (Marshall *et al.*, 2003). For treefrog, *H. ebraccata*, aggressive calls are graded: as the distance between interacting males decreases, the duration of the introductory notes gradually increases while the number and duration of click notes decrease (Wells and Schwartz, 1984; Wells, 1989). Since the aggressive calls are less attractive to females than the advertisement calls, producing aggressive calls could reduce a male's chances of attracting a mate (Bard and Wells 1987).

Compared with the conspecific advertisement calls, the aggressive calls are generally less stereotyped because they do not function in species recognition. Indeed, temporal features such as pulse repetition rate and the number of pulses are much more variable in the aggressive calls than in the advertisement calls (Schwartz and Wells, 1984; Littlejohn, 2001; Owen, 2003). For instance, if the advertisement call is a short, tone-like peep, the aggressive call is an even shorter click, or if the former consists of a series of repeated notes, the latter composites of irregular trains of short pulses. The advertisement calls of the Angola forest treefrog (*Leptopelis viridis*) are short clicks, whereas the aggressive calls are about twice as long and have a slightly lower dominant frequency (Steffen *et al.*, 2000).

### 3. Signal Complexity and Exaggeration

Some anuran males produce a single type of sexual signal, while others emit highly complex and graded sexual signals which enable males to attract females and compete with rivals (Berglund *et al.*, 1996). It is a hot research field of how and why the signal systems evolutionarily achieve their complexity. Females might prefer the acoustic complexity of signals if it can

predict signalers' quality (Hebets and Papaj 2005; Searcy and Nowicki, 2005), or signals may evolve complexity to exploit females' sensory or cognitive biases (Hebets and Papaj 2005; Akre and Ryan, 2010). The third advantage of signal complexity might enhance evidently females' working memory for males' mating calls (Akre and Ryan, 2010). For some anuran species, two types of advertisement call notes have evolved so that one type of note serves to attract females while another to repel competitive males (Narins and Capranica, 1978; Littlejohn and Harrison, 1985; Zhu *et al.*, 2016). This seems to be one of the solutions for the dilemmatic situation of interferences between advertisement and aggressive calls in reproductive signaling (Bard and Wells 1987).

The signals that yielded enhanced female preference are either additions to an existing signal (i.e. adding additional notes to a call), or extensions of a signal along some dimension (spectrum, temporal feature, or amplitude) to a point beyond which males normally signal such that they do tend to make signals more attractive. In túngara frog (*Engystomops pustulosus*), soloing males tend to produce the calls with whine only, but males increase call complexity by adding chucks at the end of whines in response to vocal competition from other males. When females were given a choice between a whine-only and a whine with chucks, except competition from other males, females also preferred the latter (Rand and Ryan, 1981; Ryan 1985). By exaggerating their presence, females of this species could cause males to produce even costlier and more attractive signals by exhibiting "elicitation" behaviors (Akre and Ryan, 2011). The complexity of vocal activities can increase depending on social contexts such as chorus ponds in which males and females interact behaviorally. For instance, many anurans have repertoires consisting of distinct types of calls, and they often exhibit considerable plasticity in their use of different call elements, responding to changes in local chorus density, the presence of nearby conspecific and heterospecific callers, and to approaching females by modifying their vocal signals (Wells, 1988; Gerhardt and Huber, 2002). Exaggerated sexual dimorphism, such as long tails in birds and more acoustic components in the calls of birds and frogs, had bewildered Darwin because it was unable to be explained in the frame of the natural selection. It has been well-known that female mate choice depends on how females perceive and compare male signals so that female preference for elaborate signals generally leads to the evolution of signal exaggeration (Anderson, 1994). The second force to drive signal overemphasized is male-male competition, for instance, the male music frog can make calls with one or more notes each time than its rivals in the same ponds (Chen *et al.* 2011). This frog can produce calls consisting of up to 11 notes if he is artificially broadcasted stimuli containing nine or ten notes, while usual calls with four or five notes are

spontaneously emitted without the stimulation.

Yet such exaggeration does not evolve without limits that may include physiological extents, predation pressures, and recognition constraints (Gomes *et al.*, 2017; Hemingway *et al.*, 2019). One species of frog-eating bats localizes preys through the frog's mating call and preferentially approaches complex calls (Ryan *et al.*, 1982; Page and Ryan, 2008). Perception constraints of female discrimination can broadly impose a selective force that limits signal elaboration (Ryan, 1990; Cui *et al.*, 2016a). The female's ability to discriminate different calls depends on the signal proportional ratio rather than absolute difference, as predicted by Weber's law:  $\Delta I / I = k$  (where  $\Delta I$  is the minimum difference required in discriminating from a stimulus of magnitude  $I$ , and  $k$  is a constant) in binary choice tests (Akre *et al.*, 2011). This implies that the female cognition limits the evolution of signal elaboration while the effect, i.e. Weber's law, could be surmounted by signal complexification. In the music frog, the increases in the fundamental frequency between successive notes in the male advertisement calls, which increase the spectral complexity of the calls, enhance the female's ability to compare the number of notes between calls (Cui *et al.*, 2016a).

#### 4. Note Position

Most calls from anurans consist of different types of notes, with each playing a specific role in communication (Halliday, 2016). It is well-known that calling activity is energetically costly and may draw the attention of potential predators when attracting potential mates. Consequently, an encoding of the most important information in the initial call period can not only facilitate species discrimination and individual recognition by females but also reduce the signaler's predation risks (Yue *et al.*, 2017). In addition, the transition from silence to sound at a call's onset may be a critical feature of the call's attractiveness and/or aid localization of its source (Snedden and Greenfield, 1998). Therefore, the temporal and spectral properties of the first note in music frogs are distinctively different from those of other notes, resulting in a multidimensional scaling (Chen *et al.*, 2011). In the tree frog (*Rhacophorus zhoukaiya*), the temporal and spectral attributes of the first note provide sufficient information for females' discriminating between different individuals. Moreover, discriminant analysis shows that the fundamental frequency of the first note is sufficient to identify individuals when the data are not normalized (Fang *et al.*, 2019).

The first note effect is also supported by some electrophysiological studies in which data collection and analysis followed the event response potential (ERP) paradigm (Fang *et al.*, 2015). Music frogs spend about 100 ms to initiate the processing of neural signals after the sound stimulation onset while during this period no apparent behavioral response

can be observed. ERP component N1 (peak at ~100 ms from stimulus on) shows a large value to white noise rather than to conspecific calls. In contrast, P2 (peak around 200 ms) amplitude of ERP is higher in response to the conspecific calls than that to the white noise, implying that the neural process underlying the identification of call characteristics is accomplished within ~200 ms because of the sensitivity of P2 components to the specific features of acoustic stimuli (Shahin *et al.*, 2005). In music frogs, the average duration of the first note is about 170 ms which locates within the time scale of P2 (Chen *et al.*, 2011; Fang *et al.*, 2015). Individual characteristics such as those encoded with the numbers and other acoustic features of notes are decoded in a relatively time-consuming mode (Ryan, 2010; Cui *et al.*, 2016b).

#### 5. Auditory CNS laterality

The lateralization of brain function is the tendency for some neural functions or cognitive processes to be specialized to one side of the brain or the other. The long-held view that laterality is unique to the human cortex has been supplanted by overwhelming evidence of left-right differences in neuroanatomy and neural processing across vertebrate and even some invertebrate species (Halpern *et al.*, 2005). The vocal-auditory lateralization is considered an important step in the evolution of human languages which, furthermore, is proposed to originate evolutionarily from the vocal vertebrates (Tervaniemi and Hugdahl, 2003; Sininger and Bhatara, 2012). Both areas of Broca for speech production and Wernicke for language auditory processing locate at the left hemisphere of most human brains (Powell *et al.*, 2006).

Right-ear/left-mesencephalon predominance or briefly right ear advantage (REA) in anuran auditory signal processing is determined by behavioral and neurophysiological paradigms recently, though it has been found previously for the perception of conspecific vocal signals in birds and mammals (Beecher *et al.*, 1979; Böye *et al.*, 2005; Zucca and Sovrano, 2008). The music frogs preferentially turn to the right side in response to positive (conspecific calls with high or low sexual attractiveness) or neutral (white noise, thunder, and silence) sounds but turn to the left side to negative sounds (screech recorded from a frog bitten by a snake) when stimulated (Knight, 2015; Xue *et al.*, 2015). Accordingly, the stronger electrical activities in the left auditory mesencephalon, diencephalon, and telencephalon than the right ones are recorded with the positive and neutral sound stimulations. Several electrical neurophysiological paradigms were applied in the music frog, including mismatch negativity (MMN) (Yue *et al.*, 2017), Granger causal connectivity analysis (GCCA) (Xue *et al.*, 2016), approximate entropy (ApEn) (Liu *et al.*, 2016) and in addition, ERP in the African clawed toad (*Xenopus laevis*) (Fan *et al.*, 2018). All these analyses have confirmed the left

CNS dominance of the auditory system.

It has been suggested that REA effect was attributed to selective attention, an important step of visual and auditory recognitions (Rogers *et al.*, 2004). The division and coordination of brain functions across the hemispheres allow animals to deal with two or more different environmental inputs, such as foods and predators, at the same time (Xue *et al.*, 2015; Hausberger *et al.*, 2019). Two models for REA phenomenon have been proposed, a structural model and an attentional one for humans and mammals, while neither are able to fully explain the phenomena found in anurans. Instead, REA of vocal communication in anurans might result from the combination of structural asymmetry and attention modulation (Fang *et al.*, 2014).

In contrast with avian vocal studies in which cognitive mechanisms are the main topic, a few investigations are involved in vocal recognition in anurans. Notably, the simple model usually provides an easy way to reach the deep core (such as genes, biochemical procedures, and neuronal networks) of biological phenomena. Because of relatively simple acoustic structures in anuran calls that are completely determined by instincts, it is rational and practicable to compare evolutionary trajectories of vocal communication based on phylogenetic frames across species (Gerhardt, 2001). More field works are needed to explore new patterns in both signal coding and decoding since anurans are so diversified in their morphological features, behaviors, and habitats. Combined the neural recordings of the single units and field potentials may provide unexpected perspectives for the physical and biological significance of acoustic signals in anurans.

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