



Does common spatial origin promote the auditory grouping of temporally separated signal elements in grey treefrogs?

MARK A. BEE & KASEN K. RIEMERSMA

Department of Ecology, Evolution, and Behavior, University of Minnesota, Twin Cities

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'Sequential integration' represents a form of auditory grouping in which temporally separated sounds produced by the same source are perceptually bound together over time into a coherent 'auditory stream'. In humans, sequential integration is important in music and speech perception. In this study of the grey treefrog, *Hyla chrysoscelis*, we took advantage of female selectivity for advertisement calls with conspecific pulse rates to investigate common spatial location as a cue for sequential integration. We presented females with two temporally interleaved pulse sequences with pulse rates of 25 pulses/s, which is half the conspecific pulse rate and more similar to that of *H. versicolor*, a syntopically breeding heterospecific. We tested the hypothesis that common spatial origin between the two pulse sequences would promote their integration into a coherent auditory stream with an attractive conspecific pulse rate. As the spatial separation between the speakers broadcasting the interleaved pulse sequences decreased from 180° to 0°, more females responded and females had shorter response latencies and travelled shorter distances en route to a speaker. However, even in the 180° condition, most females (74%) still responded. Detailed video analyses revealed no evidence that patterns of female phonotaxis resulted from impaired abilities to localize sound sources in the spatially separated conditions. Together, our results suggest that females were fairly permissive of spatial incoherence between the interleaved pulse sequences and that common spatial origin may be only a relatively weak cue for sequential integration in grey treefrogs.

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A fundamental question in sensory biology, and one that is central to understanding the mechanisms of animal communication (Feng & Ratnam 2000; Hulse 2002; Bee & Micheyl, *in press*), is how do brains parse continuous streams of sensory information into perceptually distinct units? The processes by which the auditory system solves this problem are often referred to as 'auditory scene analysis' (Bregman 1990; Hulse 2002; Bee & Micheyl, *in press*). Analysing acoustic scenes involves integrating or 'grouping' sounds that originate from a single source into perceptually coherent 'auditory streams' or 'auditory objects' that can be attended to and perceptually segregated from other sounds in the environment (Bregman 1990; Carlyon 2004; Bee & Micheyl, *in press*).

Two forms of perceptual integration are important in human auditory scene analysis (Bregman 1990). 'Simultaneous integration' refers to the perceptual grouping of different, simultaneously occurring components of the frequency spectrum (e.g. harmonics, formants) into a representation of a single sound source. 'Sequential integration' on the other hand involves the integration of temporally separated sounds from one sound source (e.g. syllables, words, musical notes) into a coherent auditory stream and their segregation from other intervening and overlapping sounds from other sources. Both simultaneous and sequential integration are important in music and speech perception by humans and in allowing human listeners to solve the so-called 'cocktail party problem,' which refers to the difficulty we sometimes have understanding speech in noisy social environments (reviewed in Bregman 1990; Bee & Micheyl, *in press*). Numerous studies have investigated the auditory grouping cues, including common spatial origin and various acoustic

Correspondence: M. A. Bee, Department of Ecology, Evolution, and Behavior, University of Minnesota, 100 Ecology, 1987 Upper Buford Circle, St Paul, MN 55108, U.S.A. (email: mbee@umn.edu).

cues, that humans use to perform simultaneous and sequential integration (reviews in Bregman 1990; Darwin & Carlyon 1995; Cusack & Carlyon 2004; Bee & Micheyl, in press).

While auditory scene analysis constitutes a major paradigm in studies of human hearing and speech communication (Bregman 1990; Carlyon 2004; Cusack & Carlyon 2004), few studies have investigated similar processes in the acoustic communication systems of nonhuman animals (Feng & Ratnam 2000; Hulse 2002; Bee & Micheyl, in press). Anuran amphibians (frogs and toads) represent one taxonomic group for which aspects of auditory scene analysis may be important for communication (Hulse 2002). Although the cocktail-party-like listening conditions in a frog breeding chorus can impair auditory perception (Gerhardt & Klump 1988; Wollerman 1999; Schwartz et al. 2001; Wollerman & Wiley 2002; Bee 2007, 2008; Bee & Swanson 2007), the advertisement calls of male frogs nevertheless effectively mediate species recognition, source localization, female mate choice, male–male assessment, and even individual recognition under the noisy conditions of a breeding chorus (reviews in Gerhardt & Bee 2006; Wells & Schwartz 2006).

Many frogs produce vocalizations consisting of sequentially produced call types (Ryan 1985; Larson 2004) or temporally repeated pulses (Gerhardt 1991; Castellano & Giacoma 1998; Howard & Young 1998; Friedl 2006). In frogs with pulsed advertisement calls, the rate of temporally repeated pulses is often an important acoustic property for species recognition (reviewed in Gerhardt & Huber 2002), and the number of pulses per call can serve as an honest indicator of male genetic quality (Welch et al. 1998). Although the sequential integration of temporally separated signal elements is potentially important for species recognition and mate choice in frogs, we still know very little about the cues that promote sequential integration (but see Schwartz & Gerhardt 1995; Farris et al. 2002, 2005). In this study, we tested the hypothesis that common spatial origin functions as an auditory grouping cue that promotes the sequential integration of temporally repeated pulses in the context of call recognition by females of Cope's grey treefrog, *Hyla chrysoscelis*.

METHODS

Study System and Experimental Rationale

Cope's grey treefrog is the diploid member of the cryptic diploid–tetraploid grey treefrog species complex; the eastern grey treefrog, *H. versicolor*, is the tetraploid (Ptacek et al. 1994; Holloway et al. 2006). These two species breed syntopically throughout much of their common range in North America, including Minnesota, where this study was conducted. A great deal is already known about the acoustic properties that mediate species recognition by females of both species (reviewed in Gerhardt 2001). The advertisement calls of male *H. chrysoscelis* comprise a series of pulses produced at a species-typical rate of about 35–50 pulses/s (Gerhardt 2001). The pulsed advertisement calls of *H. versicolor* are spectrally similar but have pulse

rates of 19–24 pulses/s, which is about half as fast as those of *H. chrysoscelis* calls (Gerhardt 2001). Females of both species show robust selectivity for conspecific pulse rates (Gerhardt & Doherty 1988; Gerhardt 2001; Bush et al. 2002; Schul & Bush 2002). We took advantage of a female's pulse rate selectivity to test the hypothesis that spatial coherence between the temporally separated pulses of a male's calls promotes sequential integration. We presented females with two temporally interleaved pulse sequences broadcast at angular separations of 180°, 90°, 45° or 0°. Each pulse sequence was delivered at a rate that was about half the normal pulse rate of *H. chrysoscelis* calls, and more similar to the unattractive pulse rate of heterospecific *H. versicolor* calls. We predicted that as the spatial separation between the two sequences decreased from 180° to 0°, females would be more likely to integrate the two sequences into a coherent auditory stream with the attractive pulse rate of conspecific calls. Hence, the underlying assumption of our experimental approach was that females would show greater relative phonotaxis under conditions that promoted auditory grouping.

General Procedures

Details regarding our field sites, our procedures for collecting, handling and testing females, and the sound chamber and playback system used for conducting experiments have been fully described in Bee (2007). Briefly, we made nightly collections of females in amplexus between 5 May and 29 June 2006 from several local breeding populations. They were returned to the laboratory, used as subjects in several phonotaxis tests, and then returned to their original location of capture, usually within 1–3 days of collection.

We conducted phonotaxis tests in a circular test arena (2-m diameter) located inside a walk-in, hemi-anechoic sound chamber. The sound chamber was temperature controlled and all phonotaxis tests were performed at 20 ± 2 °C. The walls of the circular test arena were constructed from hardware cloth (60 cm height) and covered by visually opaque, but acoustically transparent, black cloth. The perimeter of the arena floor was divided into 24 15° bins. Playback speakers (A/D/S L310) were positioned on the floor of the chamber just outside the arena wall, centred in a 15° bin and aimed towards the centre of the arena. Before testing, females were placed in a 20 °C incubator and their body temperatures were allowed to reach 20 ± 1 °C. At the beginning of a test, we removed the female from the incubator and placed her in an acoustically transparent release cage (9 cm diameter) on the floor in the centre of the test arena. After a 1-min acclimation period, we started broadcasts of the acoustic stimulus, which was broadcast as a continuous loop during the test. After four repetitions of the loop, we remotely released the female. Groups of three to five females were typically tested in sequence, with one female being tested while the other females waited in the incubator during a 5–15 min 'time-out' between tests. The absolute positions of the playback speakers around the perimeter of the circular arena were systematically varied between groups of

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