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Giant pandas perceive and attend to formant frequency variation in male bleats

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Animals often use acoustic signals to assess the physical characteristics of conspecifics in reproductive contexts. Here, we manipulated two components of male giant panda bleats, the formant frequencies (an acoustic cue to size) and the fundamental frequency, to examine male and female responses to bleats characterized by different combinations of these acoustic components. Our results revealed that male giant pandas had greater looking responses and tended to respond faster to bleats with higher formants simulating small adult males. In contrast, females had greater looking responses to bleats with lower formants simulating large adult males. In addition, there was no interaction between the value of the fundamental frequency and the observed response of male and female giant pandas to formant frequency variation in male bleats. Taken together these findings indicate that formants are functionally relevant to male and female giant pandas, and suggest that the level of the fundamental frequency in male bleats does not significantly affect how receivers perceive formant frequency variation. Furthermore, the sex differences in response direction are consistent with the notion that giant pandas could be using formants as cues to the caller's sex, through the correlation with body size, during the breeding season.

Many nonhuman animal species use acoustic signals to assess the physical characteristics of conspecifics (Hauser 1996). In particular, acoustic cues present in species-specific animal vocalizations may encode information about some aspect of the caller's phenotype important in reproductive contexts (Andersson 1994). The application of the source-filter theory of vocal production (Fant 1960) to nonhuman animals explicitly links specific acoustic components of animal vocalizations to their production mechanisms (reviewed in Fitch & Hauser 2002). Allied to this, progress in bioacoustics and digital signal processing allows us to examine, extract and manipulate specific acoustic components, so that animal calls can be resynthesized in which the acoustic parameter of interest has been manipulated whilst leaving all others unchanged. Theoretically, by playing back these resynthesized calls and observing behavioural responses, the functional relevance of particular acoustic components can be determined.

For example, a number of recent studies have shown that formants (the resonance frequencies of the vocal tract) provide reliable information on the caller's body size in several nonhuman mammal species (Fitch 1997; Riede & Fitch 1999; Reby & McComb 2003; Harris et al. 2006; Sanvito et al. 2007; Vannoni & McElligott 2008; Charlton et al. 2009b) because of a close relationship between the formant spacing, the caller's vocal tract length (VTL) and overall body size (Fitch 2000). Further work, using resynthesized playback stimuli, has shown that nonhuman mammals attend to variation in size-related formant information in species-specific calls (Reby et al. 2005; Fitch & Fritz 2006; Charlton et al. 2007a, b, 2008a, b; Ghazanfar et al. 2007; Taylor et al. 2010), suggesting that formants could have functional relevance as acoustic cues to body size in several nonhuman species-specific communication systems. Furthermore, this reliable information on body size may allow receivers to gauge the caller's sex in species where males and females differ in body size (Rendall et al. 2004; Charlton et al. 2009b).

The relevance of fundamental frequency (F0) variation to nonhuman mammals is less clear. F0 is perceived as the basic pitch of the vocalization, and given that it is a highly salient and variable component of mammal calls it may signal important attributes of the caller, such as its hormonal quality, maturity and social dominance (Reby & McComb 2003; Evans et al. 2008; Vannoni & McElligott 2008). Furthermore, the level of F0 may affect the perception of formants. Vocalizations with low F0s will have dense harmonic structures that should make formants more perceptually salient to receivers (Ryalls & Lieberman 1982; Owren & Rendall 2001). Notwithstanding this, only one previous study has examined how F0 affects formant perception in a nonhuman animal (Charlton et al. 2008b).

Giant pandas, *Ailuropoda melanoleuca*, are solitary mammals that rely on effective communication to coordinate their once

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yearly mating activities (Schaller et al. 1985). The importance of olfaction in this species' sexual communication, possibly for stimulating male sexual motivation and recruiting potential mating partners, is well documented (Swaisgood et al. 2000, 2002, 2004). However, giant pandas also have a rich vocal repertoire that is likely to be important for mediating close-range interactions during the breeding season (Peters 1982; Schaller et al. 1985). In particular, male giant pandas produce bleat vocalizations at high rates when they encounter oestrous females (Peters 1982; Kleiman 1983), indicating that these calls are important in reproductive contexts.

Whereas earlier work on giant panda vocal communication concentrated on outlining the vocal repertoire and ascribing broad functional categories to vocalizations (Peters 1982, 1985; Kleiman 1983; Schaller et al. 1985), recent studies have shown that giant panda bleats are individually distinctive and that they encode information on the caller's sex, age and body size (Charlton et al. 2009b, c). In particular, formant frequency spacing is a reliable acoustic cue to the caller's sex and male body size in giant panda bleats (Charlton et al. 2009b). Further studies have shown that female giant pandas are able to discriminate between single bleats from different male callers (Charlton et al. 2009a), implying an ability in giant pandas to attend to the finer acoustic features of male bleats, such as the formants and F0.

In the current study, we used resynthesis techniques to create playback stimuli in which we independently manipulated the formant frequencies and the mean F0 of male giant panda bleats, while leaving all other acoustic parameters unchanged. We then used these stimuli in playback experiments to examine the behavioural response of male and female giant pandas to male bleats characterized by different combinations of these acoustic components. Body size is a key determinant of competitive ability in many species (Owings & Morton 1998) and females commonly prefer larger males in mate choice contexts (Ryan 1980; Charlton et al. 2007a). Consequently, it may be adaptive for male and female giant pandas to adjust their behavioural responses according to the size-related formant information broadcast in male bleats during the breeding season. In addition, because formant spacing is consistently higher in female giant panda bleats than it is in male bleats and other acoustic parameters like F0 and duration do not differ between the sexes (Charlton et al. 2009b), giant pandas could use formants to assess a caller's sex during the breeding season.

If giant pandas use formants as acoustic cues to male body size, we predicted that both males and females would pay greater attention to bleats with low formants simulating large adult males that advertise more threatening rivals and high-quality mates to males and females, respectively. However, if formants are used as cues to the caller's sex, we predict that male and female giant pandas will have different directions of response. More specifically, we predict that males will show greater attention to bleats with high formants more likely to originate from female callers, and females will show greater attention to bleats with low formants representing male callers. In addition, when bleats are delivered at low F0s the density of harmonic sampling of the formant envelope is increased, which may be expected to increase the salience of the formant structure (Ryalls & Lieberman 1982; Owren & Rendall 2001). Accordingly, we predicted that the greatest differential responses to formant variation would occur when the F0 of male bleats was lowest.

METHODS

Experimental Site and Animals

The playback experiments were conducted at the Chengdu Research Base of Giant Panda Breeding (CRBGPB), Chengdu, P.R. China during the 2008 and 2009 breeding seasons (February–May). A total of 20 adult giant pandas (12 females, 8 males) were used as subjects in the playback experiments. The study population consisted of captive-born animals and one wild-caught male. Females were aged from 6 to 19 years (mean = 11.8 years) and males ranged in age from 5 to 22 years (mean = 11.5 years). Although subjects were housed separately, they all had previous vocal interactions with male and female giant pandas in adjacent enclosures. The playback experiments were conducted when the subjects were in their respective outdoor yards, each measuring approximately 20 m^2.

Selection of Bleats for Resynthesis

To create the playback stimuli we selected five single giant panda bleats from each of four adult males that were aged 10–17 years (mean = 13.5 years) and unfamiliar to the current residents at the CRBGPB. These males were previously recorded during and just prior to the spring breeding season at four institutions (CRBGPB; Zoo Atlanta, U.S.A.; San Diego Zoo, U.S.A.; Smithsonian National Zoological Park, U.S.A.) using an Audio-Technica AT835b microphone and a TASCAM HDP2 portable solid-state digital recorder at distances of 3–10 m. The recordings were transferred to an Apple Macintosh Macbook computer, saved as AIFF files, and normalized to 100% peak amplitude (sampling rate: 48 kHz; amplitude resolution: 16 bits). Aside from differences in formant frequency spacing, male giant panda bleats have higher jitter and average peak-to-peak variation in F0 modulation than female bleats (Charlton et al. 2009b). Accordingly, to allow us to test our two hypotheses (the use of formants for sex versus male size assessment), we chose male bleats with jitter and average peak-to-peak variation in F0 modulation that fell within the expected ranges for male and female giant pandas (Charlton et al. 2009c). The playback sequences consisted of five single bleats each separated by 10 s from the four male exemplars (mean total duration = 46 s; range 44–49 s). The mean intensity of all the playback sequences was scaled to 70 dB.

Acoustic Analyses

To determine the appropriate readjustment factors by which to resynthesize the playback stimuli, we initially measured the formant and F0 values for each bleat using Praat 5.0.29 DSP package (Boersma & Weenink 2005).

Formant frequency and spacing estimation

The frequency values of the first six formants were measured using Linear Predictive Coding (LPC; 'To Formants (Burg)' command in Praat). The following analysis parameters were used: time step: 0.01 s; window analysis: 0.2 s; maximum formant value: 3800–4000 Hz; maximum number of formants: 5–6; pre-emphasis: 50 Hz. To measure the lower three formants more accurately we ran another analysis using the following parameters: time step: 0.01 s; window analysis: 0.2 s; maximum formant value: 2000 Hz; maximum number of formants: 3; pre-emphasis: 50 Hz, and discarded formants 1–3 from the first analysis. The formant values from both analyses were then combined and used to estimate the formant spacing (ΔF) during each bleat using the linear regression method outlined in Reby & McComb (2003). The vocal tract length (VTL) of a caller can then be estimated using the equation: $\mathrm{VTL} = c/2\Delta F$ where c is the approximate speed of sound in the mammalian vocal tract (350 m/s) (Titze 1994).

The linear regression method described by Reby & McComb (2003) plots the expected formant positions against actual measured values, and this needs a vocal tract model to provide the expected formant values to regress the observed values against.