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Size communication in domestic dog, *Canis familiaris*, growls

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In many species, body size is a key determinant of the outcome of agonistic interactions, and receivers are expected to attend to size cues when assessing competitors' signals. Several mammal vocalizations, including domestic dog growls, encode reliable information about caller body size in the dispersion of formant frequencies. To test whether adult domestic dogs attend to formant dispersion when presented with the growls of their conspecifics, we played recordings of resynthesized growls where the size-related variation in formant frequency spacing was manipulated independently of all other parameters. Subjects from three different size groups (small, medium and large dogs) were presented with playbacks of growls where formant frequencies had been rescaled to correspond to a dog 30% smaller or 30% larger than themselves. While large dogs systematically displayed more motivation to interact when growls simulated a smaller intruder, small dogs did not respond differentially to the playback conditions. However, the small dogs responded significantly less than all other size groups to both playback conditions. Our results suggest that domestic dogs are able to perceive size-related information in growls, and more specifically that they are able to adapt their behavioural response as a function of the perceived intruder's size relative to their own.

Recent studies of animal vocal communication have shown that vocal signals encode information on the physical characteristics of callers such as body size, age and sex (Fitch 1997; Fitch & Reby 2001; Reby & McComb 2003; Pfefferle & Fischer 2006; Charlton et al. 2009). The acoustic expression of physical characteristics is often reliable or 'honest', because vocal production mechanisms impose biophysical constraints on specific acoustic parameters, leading to predictable covariation between these parameters and the physical attributes of the animals that produce them (Fitch 2002; Fitch & Hauser 2002). One of the most studied sources of acoustic variation in mammals is body size, and more specifically the effect of body size on the vocal tract resonances or 'formant' frequencies of vocalizations (Fitch 1997; Riede & Fitch 1999; Reby & McComb 2003; Harris et al. 2006; Sanvito et al. 2007; Vannoni & McElligott 2008). As body size is a determinant of resource-holding potential, fighting ability and reproductive success (Owings & Morton 1998), acoustic signals that provide an index of caller body size are potentially crucial (Fitch 2002; Reby & McComb 2003).

The basis for the acoustic expression of body size is rooted in the mammalian mechanisms of vocal production. Phonation starts when air expelled from the lungs travels through the vocal folds (the glottis) in the larynx, causing a pressure drop across the larynx that results in flow-induced oscillation of the vocal folds. This oscillation occurs at a rate of vibration known as the fundamental frequency (F0) and creates a modulated waveform (the glottal wave), which constitutes the 'source' component of most vocalizations (Titze 1994). The glottal wave subsequently travels through the vocal tract, which acts as a filter, generating broad bands of energy called 'formants' at its resonant frequencies (Fant 1960; Titze 1994). The resonant properties of the vocal tract are determined by its physical attributes, specifically its length (Titze 1994; Fitch 1997; Riede & Fitch 1999). The relative positions of formants, and in particular formant dispersion, in the frequency domain are thus directly linked to vocal tract length (Fitch 1997; Riede & Fitch 1999; Reby & McComb 2003), which in turn is typically correlated with overall caller body size owing to anatomical constraints on vocal tract growth, specifically vocal tract length and shape (e.g. rhesus macaques, *Macaca mulatta*: Fitch 1997; domestic dogs: Riede & Fitch 1999). Formant dispersion (Fitch 1997) has thus been shown to be a reliable index of caller body size in several species (domestic dogs: Riede & Fitch 1999; Taylor et al. 2008; red deer, *Cervus elaphus*: Reby & McComb 2003; Reby et al. 2005; rhesus macaques: Fitch 1997): larger individuals with longer vocal tracts produce lower and more closely spaced formants, while smaller individuals with shorter vocal tracts produce higher and more widely spaced formants.

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Although several mammalian species have been shown to attend to size-related variations in formant dispersion (e.g. red deer: Reby et al. 2005; Charlton et al. 2007a, b, 2008a, b; rhesus macaques: Fitch & Fritz 2006; Ghazanfar et al. 2007), size information may be particularly relevant in species where artificial breeding has created an exceptionally large range of size variation, such as the domestic dog (Coppinger & Coppinger 2001; Sutter et al. 2007). Growling, one of the most common vocalizations in the domestic dog repertoire (Cohen & Fox 1976), is contextually appropriate for investigating the perception of size-related acoustic variation, as it generally occurs in territorial and agonistic contexts where caller body size may have important implications for the outcome of interactions (Fox 1971; Cohen & Fox 1976). Moreover, growls are structurally ideal for the auditory discrimination of formant frequencies (Riede & Fitch 1999; Taylor et al. 2008) as they are broadband signals in which the broad spread of energy across many different frequencies makes it more likely that any particular resonance will have an observable acoustic effect (Ryalls & Lieberman 1982; Nowicki & Marler 1988; Fitch & Hauser 1995).

Digital methods of signal manipulation, such as PSOLA (Pitch-Synchronous Overlap and Add) enable the independent manipulation of one or more target parameters in a vocal signal (e.g. formant dispersion, F0 and/or signal duration), while all other dimensions are left intact (see Charlton et al. 2007a for details about using PSOLA for resynthesizing mammal vocalizations). The use of resynthesized (rather than natural) stimuli means that variation in receiver response can be controlled by the acoustic standardization of nontarget parameters. In a previous study, we used resynthesized dog growls to demonstrate that human listeners are able to make accurate judgements about dog body size on the basis of formant dispersion in isolated growls (Taylor et al. 2008). Based on this evidence, and on research in other species (e.g. red deer: Reby et al. 2005), it is thus expected that the formant dispersion of domestic dog growls is also a salient cue in intraspecific communication.

In the present study, we tested whether adult domestic dogs attend to formant dispersion in conspecific growls. We conducted a playback experiment where formant dispersion was resynthesized using PSOLA. Each dog was exposed to two sets of paired stimuli. The first set of stimuli consisted of growls that were resynthesized to mimic a dog 30% larger than the subject, and the second set consisted of the same exemplars resynthesized to mimic a dog 30% smaller than the subject. We predicted that dogs would respond differently to the two types of stimuli, thereby indicating that they are able to perceive size-related variation in acoustic information. We also looked at relative response differences between the three groups of subjects (small, medium and large dogs).

METHODS

Subjects

Twenty-six adult domestic dogs were used as subjects. They were described by their owners as nonaggressive towards humans and were recruited via voluntary response to an advertisement for the study in a local veterinary surgery. They had not taken part in any previous vocal communication recordings or playback experiments. We weighed them on PS250 veterinary floor scales, and split them into three weight categories (small: under 9.9 kg; medium: 10–19.9 kg; large: over 20 kg). Table 1 gives their ages, breeds and weights.

Playback Stimuli

We recorded growls from a second sample of 26 dogs that were not related or known to the subject dogs. Recordings were made in a standardized context in which A.M.T. entered the dog's home to trigger a territorial vocal response (similar methods have been used in previous dog vocal communication studies: Yin & McCowan 2004; Pongrácz et al. 2005; Taylor et al. 2008). Although adult domestic dogs may also growl in playful contexts (Cohen & Fox 1976; Taylor et al. 2009), such growls were not included in the present study. Recordings were made between

Table 1
Subject information

Subject group	Subject name and breed	Age (years)	Weight (kg)	Sex
Small	Annabelle (King Charles spaniel)	9	7.2	Female
	Bobby (terrier)	5	5.1	Male
	Lotty (King Charles spaniel)	7	8.1	Female
	Maggie (Jack Russell terrier)	12	7.2	Female
	Manu (terrier)	5	6.2	Male
	Rocky (miniature dachshund)	1	8	Male
Medium	Burton (springer spaniel)	2	15.2	Male
	Diesel (Staffordshire bull terrier)	3	18.0	Female
	Ella (cocker spaniel)	2	15.4	Male
	Millicent (Shetland sheepdog)	9	12	Female
	Missy (border collie)	3	17.2	Female
	Sidney (Staffordshire bull terrier)	2	12	Female
Large	Carmen (flat-coated retriever)	5	25	Female
	Hunter (Labrador)	5	39	Male
	Kenzo (German shepherd dog)	5	38	Male
	Mystral (German shepherd dog)	5	37	Male
	Samson (rottweiler)	4	35.2	Male
Nonrespondents	Astra (chihuahua)	11	4.5	Female
	Bella (Golden retriever)	8	30	Female
	Dougal (Staffordshire bull terrier)	3	18.4	Male
	Ellie (Labrador)	2.5	30	Female
	Gertrude (English bull terrier)	2	21	Female
	Johnny (standard schnauzer)	11	25	Male
	Lily (border collie)	1	19	Female
	Poppy (Yorkshire terrier)	5	4.9	Female
	Trevor (Staffordshire bull terrier)	3.5	18.1	Male