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.

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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

January and March 2007 with a Sennheiser MKH 416 directional microphone attached to a TASCAM HD-P2 solid-state portable stereorecorder. The microphone was typically held at around 1 m from the dog's head, although there was a small level of variation (to a maximum of 30 cm) owing to uncontrollable head movements. Recording levels were manually adjusted at the start of each recording session. Recordings were transferred onto an eMac 1.42 GHz PowerPC G4 for digital processing, and only clearly defined growls (in which there was no background noise) were selected for the playback experiment. A unique exemplar was selected for each subject, with the recorded dog and the subject dog being matched for size (breed type) and weight (±1 kg). This served both to prevent sacrificial pseudoreplication and to standardize the procedure so that each growl was resynthesized only twice from its natural form: once to mimic a dog 30% larger than the selected subject, and once to mimic a dog 30% smaller than the subject (see Fig. 1 for an example of resynthesized stimuli). All resynthesized stimuli reflected callers within the natural range of variation (which spans approximately 80 to 300 Hz; Taylor et al. 2008). The resyntheses were performed with a Praat 4.4.32 script (Praat acoustic analysis freeware by P. Boersma & D. Weenink, Institute of Phonetic Sciences, University of Amsterdam, The Netherlands), running a PSOLA-based algorithm to rescale formant frequencies without affecting any other acoustic variables in the signal. The resynthesized growls sounded natural and similar stimuli have been successfully used in a psychoacoustic experiment involving human participants (Taylor et al. 2008).

Experimental Procedure

The playback experiments took place between March and June 2007. A repeated measures design was used, in which subjects took part in two playback conditions, which were counterbalanced to account for presentation order. All subjects were tested individually at their home by an experimenter that they had met on at least two prior occasions without experimentation. The experiments took place inside the house, in the main living area. An Anchor Liberty loudspeaker was hidden behind a screen that blocked the view of both the loudspeaker and of the front door of the house. A Sony Carl Zeiss Vario-Sonnar digital camcorder was used to film the experiment. Subjects were then allowed to settle in a familiar location on a loose lead (so that they would not be able to run out of sight or search for the location of the stimuli). Once the dogs were fully settled (i.e. not showing any investigative behaviours towards the experimenter or visible equipment), the loudspeaker played back the stimuli for the first condition at a standardized mean sound pressure level of 53 dB (±2 dB, as measured at 1 m by a CEL-414 Precision Impulse Sound Level Meter on C channel). Pilot trials in March 2007 showed that dogs remained in a more vigilant/attentive state for approximately 1 h after the playback of stimuli, so at least 2 h were left before presentation of the second condition. The dogs were always fully settled before the second condition was presented. Finally, the video data were analysed using Gamebreaker digital video analysis software version 5.1 (Sportstec, Warriewood, NSW, Australia) over a 30 s period following each trial.
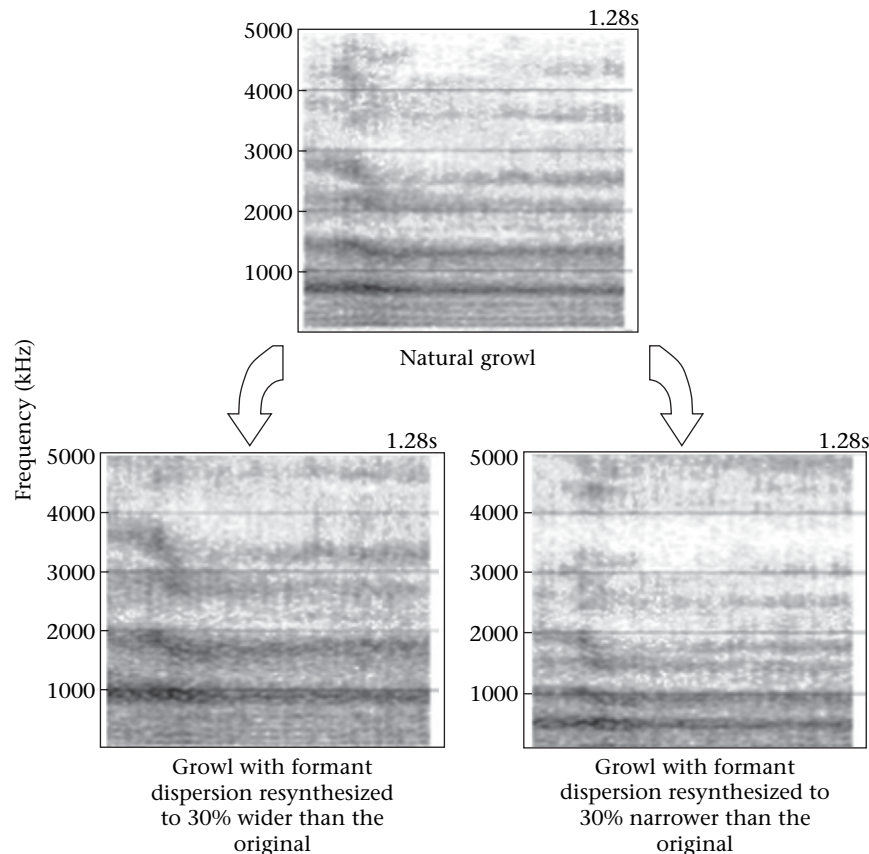

Figure 1. Spectrograms (window length: 0.08 s; time step: 0.002 s; dynamic range: 60 dB) of one set of playback stimuli, showing the original exemplar and both classes of resynthesized growl stimuli.

Table 2
Behaviours given in response to the playback stimuli

Behaviour	Definition and scoring	Function
Head cocking	Rotational movement of the head. The head is generally rotated and held in position in response to auditory stimulation. This behaviour was scored as duration of occurrence (s)	Response indicating an attempt to localize a sound after auditory stimulation (Neville 1976; Cantalupo et al. 2002)
Tail wagging	Continuous wagging of the tail. Measured as duration of occurrence (s)	Response to external stimulation as an indication of positive inner state or inquisitiveness. Tail wagging also occurs as an appeasing behaviour when approaching dominant individuals (Fox 1971)
Vocal response	Barking and whimpering in response to the playbacks. Scored as duration (s) to account for the intensity of the vocal response	See bouts of barking and whimpering below
Bouts of barking	Sequential barking without audible interbark interval (Yin 2002). Counted in number of occurrences as a continuous variable	Graded vocalization that can occur in both positive (happy, playful) and negative (anxious, territorial) social situations (Cohen & Fox 1976; Yin 2002)
Whimpering	Sequential whimpers without audible interwhimper interval. Counted in number of occurrences as a continuous variable	Serves as a social distance-reducing signal and occurs primarily in social contexts in which dogs seek to approach or greet another dog or human. In addition, whimpering may also be used to appease familiar dominant individuals (Cohen & Fox 1976)
Growling	Growls without audible intergrowl interval. Counted in number of occurrences as a continuous variable	Occurs primarily in negative social contexts, such as agonistic interactions or defensive situation (Cohen & Fox 1976)

Behavioural and Statistical Analyses

Out of 26 subjects, nine gave no behavioural response at all to either of the conditions. This was not affected by the size of the subject (see Table 1), and is more likely to reflect individual differences in temperament. Because the aim of our study was to assess behavioural differences in a repeated measures design, these subjects were removed from the sample. Thus, the results presented and discussed henceforth concern only dogs that responded to the experimental conditions.

Several types of behavioural response were observed consistently across subjects (Table 2). The variables quantifying these responses were reduced into latent factors using a principal components analysis (PCA) with varimax rotation with SPSS 11 for Mac OSX (SPSS Inc., Chicago, IL, U.S.A.). As the two emerging factors were normally distributed, mixed-effects analyses of variance were used to explore the behavioural responses given to the playbacks, with playback condition (growl typical of a small dog versus growl typical of a large dog) as a repeated measure and subject weight (small, medium or large) as a between-subjects variable. The model also controlled for the effects of playback presentation order, subject age and subject sex.

RESULTS

The PCA identified two latent factors of highly correlated behaviours (Table 3). These two factors accounted for 59.32% of the total variance (overall significance of the PCA model: $P < 0.001$).

Table 3
Component matrix showing the results of a factor analysis summarizing the behavioural responses given to the playback conditions

	Factor 1 (motivation to investigate)	Factor 2 (defensive response)
Head cocking	0.433	0.729†
Vocal response	0.881*	−0.189
Tail wagging	0.373	−0.461
Bouts of barking	0.468	0.746†
Whimpering	0.652*	−0.450
Growling	−0.203	0.542†

* Behaviours with the strongest loads (over 0.5) contributing to factor 1.
† Behaviours with the strongest loads (over 0.5) contributing to factor 2.

The first factor accounted for 41.74% of the variance (with an eigenvalue of 2.02), and was characterized primarily by duration of vocal response and bouts of whimpering. The combination of barking and whimpering in the same vocal sequence (see Cohen & Fox 1976; Yin 2002), alongside the negative correlation with aggressive behaviours (such as growling), suggests that the behaviours contributing to the first factor represent a nonaggressive motivation to interact with the unseen conspecific. We therefore labelled the first factor 'motivation to investigate'.

The second factor accounted for a further 17.58% of the variance (with an eigenvalue of 1.54) and was characterized by head cocking, bouts of barking and growling (Table 2). Together, the behaviours defining the second factor (and especially the combination of barking and growling in the same vocal sequence; see Fox 1971; Cohen & Fox 1976; Yin 2002; Taylor et al. 2009) form a typical territorial/guarding response. This is further supported by the negative loading of positive social behaviours such as tail wagging or whimpering. We therefore labelled the second factor 'defensive response'.

Playback condition significantly affected the motivation to investigate ($F_{1,12} = 8.168$, $P = 0.013$). Moreover, there was a significant interaction effect between the motivated response and subject weight. Large dogs were more motivated in response to playbacks mimicking dogs smaller than themselves than to playbacks mimicking dogs larger than themselves ($F_{1,12} = 7.421$, $P = 0.017$). There were no other interaction effects and no effects of presentation order ($F < 1$), subject age ($F < 1$) or subject sex ($F < 1$). When we compared the subject groups, small dogs were found to show less motivation to investigate than all other subject groups in response to both playback conditions ($F_{1,12} = 9.242$, $P = 0.014$). The defensive response, on the other hand, was not significantly influenced by playback condition ($F < 1$), presentation order ($F < 1$), subject weight ($F < 1$) or subject sex ($F < 1$).

DISCUSSION

Large dogs showed consistent behavioural differences in their responses to playbacks of growls mimicking dogs smaller than themselves compared to playbacks of growls mimicking dogs larger than themselves; however, small dogs did not respond differentially to stimuli mimicking larger versus smaller dogs. In addition small dogs were less responsive than all other size groups across both playback conditions.

The subjects gave several consistent types of behavioural responses to the playbacks, and these were summarized as two separate sets of highly correlated behaviours. The first set of behaviours was characterized primarily by barks and whimpers (with an absence of negative social behaviours such as growls). Barks are a graded vocalization that can occur in both positive and negative social contexts (Yin 2002; Taylor et al. 2009); however, whimpers are specifically used to greet or approach both conspecifics and humans and to placate dominant individuals (Fox 1971; Cohen & Fox 1976). The occurrence of whimpers and barks in the same vocal sequence, alongside the absence of negative behaviours, suggests that the first set of behaviours showed a nonaggressive motivation to interact with the unseen intruder. A second, more aggressive set of behaviours was also observed. This second set of behaviours was characterized by head cocking, barks and growls (with an absence of positive social behaviours such as tail wagging) and most probably corresponded to a more general territorial or defensive response. While the defensive response did not vary across playback conditions or subject variables, the dogs' motivation to investigate did vary as a function of both playback condition and subject size; specifically, large dogs showed more motivation to investigate playbacks of intruders mimicking a dog smaller then themselves (widely spaced formants) than to playbacks of intruders mimicking a dog larger than themselves (closely spaced formants). These results thus indicate that domestic dogs are able to perceive size-related formant variation (as no other acoustic parameters varied between stimuli), and that large dogs are more motivated to interact with a growling intruder 30% smaller than themselves than with a growling intruder 30% larger than themselves.

Our results are in accord with a growing body of research on the spontaneous perception of size-related variation in formant frequencies (e.g. Reby et al. 2005; Charlton et al. 2007a, b, 2008a, b; Taylor et al. 2008). They also suggest that dogs are able to make behavioural decisions based on formant information relative to their own body size, while small dogs appeared to be significantly less motivated to meet the unfamiliar intruder than all other size groups across playback conditions. Although it seems unlikely that small dogs should not possess the same ability to assess body size as large dogs, it is possible that all unfamiliar conspecifics present a greater threat to small dogs than to large dogs. Indeed, because domestication has eliminated competition for resources, small dogs benefit from avoiding entering into investigatory or aggressive interactions with unfamiliar individuals, as they have nothing to gain from a confrontation with a potentially aggressive (growling) intruder. This interpretation is supported by research on the effect of domestic dog tail size and position on the behaviour of other dogs: Leaver & Reimchen (2008) also observed that only dogs larger than a Labrador retriever model gave differential behavioural responses according to experimental condition, while dogs smaller than the model did not respond differentially to different tail positions and showed lower motivation to approach or interact with the model overall. Similarly to Leaver & Reimchen's (2008) observations, our results suggest that large dogs may be generally more confident than small dogs when deciding whether to enter into an interaction with an unfamiliar conspecific, as having a larger body size reduces the cost of signalling back to intruders. This also enables large dogs to take the time to assess information about the intruder (size in the present study and motivation in Leaver & Reimchen 2008) and to adapt their behaviour accordingly.

Spontaneous perception of size-related variation in formant frequencies has been demonstrated using habituation–discrimination experiments in several species (red deer: Charlton et al. 2007a; rhesus macaques: Fitch & Fritz 2006; whooping cranes, *Grus americana*: Fitch & Kelley 2000), and these studies have shown that information encoded by formants is salient across many types of terrestrial vertebrates. Moreover, evidence that formant dispersion is used by some animals to assess caller body size can be seen in the functionally appropriate behavioural decisions made by individuals in response to playbacks of resynthesized vocalizations (Reby et al. 2005; Charlton et al. 2007b). Finally, captive rhesus macaques have demonstrated in an operant learning task that they are able to associate calls with a small formant dispersion with pictures of large (mature) conspecifics and calls with a large formant dispersion with pictures of small (immature) conspecifics (Ghazanfar et al. 2007). This provides direct evidence that some animals can make reliable cross-modal links between acoustic and visual size cues. The consistent behavioural responses given by large dogs to the playback conditions in the present study confirm that, like many other species, domestic dogs are able to perceive size-related variation in the formants of conspecific growls. Because the motivation to investigate was the strongest behavioural response overall, future studies should attempt to quantify investigatory behaviour by allowing more freedom of movement to the subjects.

Overall, our experiment demonstrated significant behavioural differences in response to stimuli in which the only acoustic differences were formant frequencies. We have thus shown not only that domestic dogs are able to perceive formants in conspecific growls, but also that their behavioural responses depend on their own body size relative to that of the intruder. Additionally, we observed some general differences in responses, based on the subject's own body size, as small dogs responded less to all playback conditions. We have thus shown that size-related variation in the formant frequencies of growls has the potential to be salient and relevant to dogs and more research is required to investigate the perceptual threshold of this information. In addition, since other acoustic dimensions of growls can vary (e.g. F0: Taylor et al. 2008; duration: Taylor et al. 2009), future studies should investigate the perceptual and functional relevance of their covariation and how it affects intraspecific communication.

Acknowledgments

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