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Orienting asymmetries in dogs' responses to different communicatory components of human speech

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Summary

It is well established that in human speech perception the left hemisphere (LH) of the brain is specialised for processing intelligible phonemic (segmental) content (e.g. [1-3]), whilst the right hemisphere (RH) is more sensitive to prosodic (supra-segmental) cues [4, 5]. Despite evidence that a range of mammal species show LH specialisation when processing conspecific vocalisations [6], the presence of hemispheric biases in domesticated animals' responses to the communicative components of human speech has never been investigated. Human speech is familiar and relevant to domestic dogs (*Canis familiaris*), who are known to perceive both segmental phonemic cues [7-10], and supra-segmental speaker-related [11, 12] and emotional prosodic cues [13]. Using the head-orienting paradigm, we presented dogs with manipulated speech and tones differing in segmental or supra-segmental content and recorded their orienting responses. We found that dogs showed a significant LH bias when presented with a familiar spoken command in which the salience of meaningful phonemic (segmental) cues was artificially increased, but a significant RH bias in response to commands where the salience of intonational or speaker-related (supra-segmental) vocal cues was increased. Our results provide insights into mechanisms of inter-specific vocal perception in a domesticated mammal, and suggest that dogs may share ancestral or convergent hemispheric specialisations for processing the different functional communicative components of speech with human listeners.

Results and Discussion

Each dog took part in one trial where they were presented with a single sound stimulus from either one of eight conditions where speech samples were re-synthesised to vary the relative salience of segmental (phonemic) vs. supra-segmental (speaker cues and intonation) information, or from one of two control conditions (Figure 1). Using the head-orienting paradigm, the sound was played simultaneously from both sides of the subject, and the direction of the subject's initial orienting response (left or right) was recorded. We obtained head-orienting responses from 25 dogs in each condition. Given that auditory information entering each ear is processed mainly in the contralateral hemisphere of the brain via the dominant contralateral auditory pathways [14], it is assumed that if the dog turns with their left ear leading in response to the sound, the acoustic input is processed primarily by the RH, whilst a right turn would indicate primary LH processing [15].

A binary logistic regression analysis identified a significant overall effect of auditory condition on head-turn direction (Wald(8) = 37.61, $p < 0.001$), indicating that the content of the acoustic signals affected the direction of hemispheric lateralisation during perception (Figure 2). There were no significant effects of subject sex ($p = 0.76$), age ($p = 0.15$), breed type ($p = 0.37$), current residence (animal shelter or private home) ($p = 0.16$), stimulus exemplar ($p = 0.23$), stimulus voice gender (where applicable) ($p = 0.70$) or test location ($p = 0.18$) on responses.

<u>Responses to speech with increased salience of meaningful segmental phonemic cues</u>

In <u>*test 1*</u>, dogs were presented with a familiar learnt command in which the original positive intonational cues were artificially degraded ('come on then' with a flat intonation =

Meaningful Speech with Neutralised Intonation). They showed a significant right head-turn response bias (Binomial test: (80% Right head-turn), p = 0.004), suggesting that when supra-segmental intonation is neutralised and segmental phonemic cues become more salient, dogs display a LH advantage.

To verify that the LH response bias was specific to the phonemic content, in *test 2* the same command was further degraded by replacing the first three formants with sine-waves (Meaningful Sine-Wave Speech), strongly reducing supra-segmental cues (emotional and speaker-related), but retaining meaningful segmental phonemic information. Here too dogs showed a significant right head-turn bias (Binomial test: (76% Right head-turn), p = 0.015), reinforcing the interpretation that in dogs the LH is sensitive to segmental phonemic information independently of the nature and naturalness of the acoustic elements composing the signal.

These observations parallel the LH bias observed in humans when processing phonemic content in natural speech (e.g. [1-3]) and sine-wave speech signals [16].

Responses to speech with increased salience of supra-segmental cues

Both speaker-related (indexical) and emotional (dynamic) cues are encoded in the supra-segmental content of the speech signal. We first tested dogs' responses to speaker-related indexical cues by exposing them to a comparable phrase with neutralised intonation, but spoken in an unfamiliar language (*test 3*: Meaningless (Foreign) Speech with Neutralised Intonation). Here the phonemic cues were unfamiliar and the intonational prosodic cues were removed, whilst indexical speaker-related cues remained intact. Dogs in this condition showed a significant left head-turn bias (Binomial test: (24% Right head-turn), p = 0.015),

demonstrating a RH advantage when processing salient speaker-related supra-segmental content in speech. Dogs are known to perceive speaker-related vocal cues such as identity [11] and gender [12], and the observed RH advantage is consistent with human RH lateralisation when processing these features [4, 17, 18].

We also tested dogs' responses to emotional prosodic cues by presenting them with a version of the original command in which the phonemic components had been removed by extracting the formants and plosives, creating unintelligible speech-like vocal stimuli with reduced speaker cues but positive emotional prosody (*test 4*: Meaningless Voice with Positive Intonation). Here too dogs showed a significant left head-turn bias (Binomial test: (28% Right head-turn), $p = 0.04$) showing that when segmental phonemic cues are neutralised and supra-segmental emotional prosodic cues become more salient, dogs also display a RH advantage. This result furthers recent neuro-imaging evidence that auditory regions in the dog's RH are sensitive to emotional valence in both conspecific calls and human non-verbal vocalisations, with increased activation in response to calls with greater positive valence [19]. Similarly, humans not only show stronger RH activation in response to emotional speech prosody and vocalisations, but also when exposed to animal vocalisations with strong affective content independently from their familiarity with the species [20], suggesting that the perception of emotional content in vocalisations, and its lateralisation to the RH, maybe be conservative across mammals.

Response to speech when both meaningful segmental phonemic and supra-segmental prosodic cues are salient

When in *test 5* dogs were exposed to intact meaningful speech containing both segmental phonemic and supra-segmental prosodic cues ('come on then' with happy intonation =

Meaningful Speech with Positive Intonation), no significant head-turn bias was found (Binomial test: (48% Right head-turn), p = 1.00). While directing dogs' attention to either of these components using manipulated speech was found to produce opposite hemispheric biases in the previous tests, the simultaneous presence of salient segmental and supra-segmental cues that characterises natural speech results in the absence of a bias at the population level [14, 21].

Do hemispheric biases relate to the communicative content of the signal?

Two competing interpretations of hemispheric asymmetries [22-24] can be applied to our observation that in dogs the LH is primarily sensitive to segmental phonemic content, whilst the RH is primarily sensitive to supra-segmental cues. *Acoustic (cue-dependent)* theories propose that in humans auditory processing areas in the RH operate at a lower temporal resolution than those of the LH, resulting in a greater preference for processing slow acoustic modulation including supra-segmental cues in speech, whilst the LH is more specialised in analysing rapidly changing auditory information such as phonemic cues. To test whether the RH bias in response to supra-segmental cues could be explained by a general preference for slow acoustic modulation we presented dogs with a sine-wave tone matching the intonation contour of the original command (*test 6*: Sine-Wave Intonation). No orientation bias was found in response to this condition (Binomial test: (56% Right head-turn), p = 0.69), signifying that the observed RH bias for supra-segmental cues in speech does not generalise to slow frequency modulation across acoustic signals. Furthermore, in our study dogs expressed opposite response biases to speech signals with equivalent spectro-temporal complexity (Meaningful and Meaningless (Foreign) Speech with Neutralised Intonation), suggesting that the LH bias in dogs' responses to meaningful

phonemic cues was not purely dependent on the increased salience of the rapidly modulated components in the signal.

Our results appear more consistent with the *functional* interpretation of lateralisation, which proposes that hemispheric specialisation is dependent on the communicative function of the acoustic content. Indeed, the observation that the LH is preferentially recruited when dogs process the phonemic cues of the highly familiar and learnt command 'come on then' is consistent with reports that the LH tends to respond to familiar or learnt patterns across mammals [25]. To clarify whether the LH bias observed in response to Meaningful Speech with Neutralised Intonation was related to the subjects' familiarity with the command (which could either be related to familiarity with the speakers' accents and/or familiarity with the phonemes independently of their meaning), or whether this bias was dependent on the learnt functional relevance of the command itself, we carried out additional tests changing either the familiarity of the speaker's accent or the familiarity of the phonemic content in the signal.

Based on the significant LH response bias obtained in the Meaningful Sine-Wave Speech condition, in which the speaker-related cues were degraded, we predicted that reducing the familiarity of the speaker's accent would not influence responses. Dogs presented with the original command with degraded prosodic cues, but spoken by a non-native British speaker (*test 7*: Meaningful Speech in an Unfamiliar Accent with Neutralised Intonation) also showed a significant right head-turn bias (Binomial test: (72% Right head-turn), $p = 0.04$), confirming that the LH response bias obtained in *test 1* was not dependent on the familiarity of the speaker's accent.

We then assessed whether LH responses were dependent on the presence of meaningful phonemic cues, or merely familiar phonemic cues, by presenting dogs with a pseudo-word phrase using the same phonemes as the original command ('thon om ken' with neutralised intonation = Meaningless Phonemes with Neutralised Intonation) (*test 8*): both the phonemes and speaker accent were familiar, but the phrase was meaningless. Dogs in this condition showed a significant left head-turn response bias (Binomial test: (20% Right head-turn), p = 0.004), which confirms that increasing the salience of segmental phonemic content in speech only generates a LH response bias in dogs if it is functionally meaningful - i.e. if it is known to trigger a specific learnt response from the animal. This is in agreement with speech perception in humans, as only intelligible speech generates a LH processing bias [3]. Our findings therefore demonstrate that in dogs, the LH also preferentially responds to phonemic content with meaningful communicative value, whilst voice or speech-like stimuli lacking this information generate RH biases.

Do hemispheric biases extend to non-vocal signals?

To test if the LH response bias to meaningful phonemic cues would generalise to non-vocal stimuli with learnt communicative value, dogs were presented with a Meaningful Whistle (*test 9*). No significant head-turn bias was found (Binomial test: (60% Right head-turn), p = 0.42), suggesting that the LH advantage for meaningful phonemic content in speech may not extend to other familiar and communicatively relevant non-vocal sounds. Whilst this result may seem in opposition with the LH advantage that characterises the perception of articulated whistled language by experienced human listeners [26], articulated whistled languages encode phonological segmental information [27] and are therefore more comparable to the Meaningful Sine-Wave Speech used in *test* 2, which also triggered a LH

bias. In contrast, the simple command whistles used in our study did not contain segmental information (they did not result from the combination of phonological units) and were therefore more comparable to the intonation contours used in *test 6*, which also failed to trigger a bias.

Finally, because stimuli used in all of the conditions eliciting a RH response bias were re-synthesised, the perceived novelty of these sounds could have generated stronger RH activation [25]. However, at least equally novel re-synthesised stimuli elicited a LH bias (e.g. Meaningful Sine-Wave Speech) or no bias (Sine-Wave Intonation). Moreover, when dogs were exposed to a novel artificial sound (*test 10*: Pink Noise) containing neither segmental nor supra-segmental frequency modulation, they showed no significant orientation bias (Binomial test: (48% Right head-turn), $p = 1.00$). Furthermore, analysis of each subject's behaviour across conditions after the sound was presented showed that the frequencies of occurrence of each of the observed behaviours (head tilt, startle, approach, looked at owner) were not associated with conditions which produced only LH or RH biases (see Supplementary Information). This suggests that the hemispheric biases did not arise from the perceived novelty or intrinsic unnaturalness associated with re-synthesised stimuli.

Conclusion

Our study demonstrates that dogs preferentially process meaningful segmental phonemic information in speech in the LH, whilst human voices lacking this information (therefore increasing the salience of prosodic and/or speaker-related cues) generate stronger RH activation. The parallel between these hemispheric biases and those reported in humans suggests that dogs may dissociate and process the communicatory components of speech in a way which is broadly comparable with humans. Further investigations using different

techniques are now necessary to identify the specific brain regions involved when dogs process speech.

The striking correspondence between dogs' and humans' hemispheric biases reported here may reflect convergent evolution if dogs have been selected to respond to human vocal signals during domestication [28]. Alternatively, they may be indicative of shared hemispheric specialisations that are present across phylogenetically distant mammal species, and expressed when exposed to functionally meaningful speech signals. To test these hypotheses more directly, further experiments could replicate our study with other domesticated (e.g. horses) vs. non-domesticated species (e.g. captive wolves) that are regularly exposed to human speech.

Experimental Procedures

Subjects

Subject animals were over six months old, healthy with no known hearing or sight problems and not aggressive towards people. Owners of dogs exposed to the English speech confirmed that their dog responded to the command 'come on then' or a similar variant. Owners of dogs exposed to whistles confirmed that they regularly whistled to call their dog and chose a comparable whistle from the available stimuli. Only dogs with no previous exposure to French were presented with Meaningless (Foreign) Speech with Neutralised Intonation or Meaningful Speech in an Unfamiliar Accent with Neutralised Intonation. An a priori power analysis conducted using G*Power [29] with power ($1 - \beta$) set at 0.80 and $\alpha = 0.05$, two-tailed, showed that a minimum sample size of N = 20 was required in each condition for detecting a medium sized effect in a binomial test. We included the first 25

dogs that reacted to the stimuli in each condition. A small proportion of subjects (N=35) failed to react to the stimuli (with an even distribution of failed responses across conditions ($\chi^2_{(9)}$ = 11.57, p = 0.24)), and were excluded from the study at the time of testing. The 250 dogs retained in the analysis included 123 females and 127 males from 63 different breeds. Ages ranged from six months to 14 years old (mean ± SD = 4.14 ± 2.96 years). 221 dogs were privately owned pets and 29 were housed in a local animal shelter.

Apparatus

Two speakers (SONY SRS-A60) were placed 1.5 m to the right and left of the centre point. The side of each speaker was counter-balanced across subjects. The speakers were connected to a laptop placed on a table 3 m from the centre point. A video camera was positioned underneath the table to record the dog's response (Figure 3). A N05CC Digital Mini Sound Level Meter was used to ensure that the speakers broadcast at the same volume. Trials were conducted at one indoor and two outdoor locations (see Supplemental Information).

Procedure

The dog was held on a loose lead by their owner (or a research assistant for shelter dogs) who was naïve to the experimental conditions. Owners positioned their dog at the centre point, facing the table, and then stood still directly behind their dog. The experimenter stood behind the table facing the dog and attracted the dog's attention by saying their name. When the dog was stationary and facing directly forwards the experimenter looked down at the laptop (to avoid providing any gaze cues) and played the stimulus once. Stimuli were presented at 65 dB in pseudo-randomised order across trials, with equal numbers of

male and female voices until 25 subjects responded in each condition. Trials ended when the dog was no longer oriented towards one of the speakers. Dogs that did not react to the sound between the stimulus onset and two seconds after the offset were recorded as non-responsive.

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures and Results, one table, one movie and one audio file.

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Figure Legends

Figure 1. Diagram showing example spectrograms and brief descriptions of each of the auditory conditions organised by hemispheric response biases. See also Audio S1 and Table S1.

Figure 2. Percentage of dogs that orientated to their left or right in each condition following the playback presentation. * indicates conditions in which the proportions were significantly different from chance (50%) at $p < 0.05$.

Figure 3. Experimental set-up with distances between the subject, speakers and experimenter. See also Movie S1.