

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

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

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19 **Summary**

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

38

39

40 **Results and Discussion**

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

52 A binary logistic regression analysis identified a significant overall effect of auditory
53 condition on head-turn direction (Wald(8) = 37.61, $p < 0.001$), indicating that the content of
54 the acoustic signals affected the direction of hemispheric lateralisation during perception
55 (Figure 2). There were no significant effects of subject sex ($p = 0.76$), age ($p = 0.15$), breed
56 type ($p = 0.37$), current residence (animal shelter or private home) ($p = 0.16$), stimulus
57 exemplar ($p = 0.23$), stimulus voice gender (where applicable) ($p = 0.70$) or test location ($p =$
58 0.18) on responses.

59 Responses to speech with increased salience of meaningful segmental phonemic cues

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

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

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

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

76 Responses to speech with increased salience of supra-segmental cues

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

84 demonstrating a RH advantage when processing salient speaker-related supra-segmental
85 content in speech. Dogs are known to perceive speaker-related vocal cues such as identity
86 [11] and gender [12], and the observed RH advantage is consistent with human RH
87 lateralisation when processing these features [4, 17, 18].

88 We also tested dogs' responses to emotional prosodic cues by presenting them with a
89 version of the original command in which the phonemic components had been removed by
90 extracting the formants and plosives, creating unintelligible speech-like vocal stimuli with
91 reduced speaker cues but positive emotional prosody (test 4: Meaningless Voice with
92 Positive Intonation). Here too dogs showed a significant left head-turn bias (Binomial test:
93 (28% Right head-turn), $p = 0.04$) showing that when segmental phonemic cues are
94 neutralised and supra-segmental emotional prosodic cues become more salient, dogs also
95 display a RH advantage. This result furthers recent neuro-imaging evidence that auditory
96 regions in the dog's RH are sensitive to emotional valence in both conspecific calls and
97 human non-verbal vocalisations, with increased activation in response to calls with greater
98 positive valence [19]. Similarly, humans not only show stronger RH activation in response to
99 emotional speech prosody and vocalisations, but also when exposed to animal vocalisations
100 with strong affective content independently from their familiarity with the species [20],
101 suggesting that the perception of emotional content in vocalisations, and its lateralisation to
102 the RH, maybe be conservative across mammals.

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

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

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

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

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

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

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

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

152 We then assessed whether LH responses were dependent on the presence of meaningful
153 phonemic cues, or merely familiar phonemic cues, by presenting dogs with a pseudo-word
154 phrase using the same phonemes as the original command ('thon om ken' with neutralised
155 intonation = Meaningless Phonemes with Neutralised Intonation) (test 8): both the
156 phonemes and speaker accent were familiar, but the phrase was meaningless. Dogs in this
157 condition showed a significant left head-turn response bias (Binomial test: (20% Right head-
158 turn), $p = 0.004$), which confirms that increasing the salience of segmental phonemic
159 content in speech only generates a LH response bias in dogs if it is functionally meaningful -
160 i.e. if it is known to trigger a specific learnt response from the animal. This is in agreement
161 with speech perception in humans, as only intelligible speech generates a LH processing bias
162 [3]. Our findings therefore demonstrate that in dogs, the LH also preferentially responds to
163 phonemic content with meaningful communicative value, whilst voice or speech-like stimuli
164 lacking this information generate RH biases.

165 Do hemispheric biases extend to non-vocal signals?

166 To test if the LH response bias to meaningful phonemic cues would generalise to non-vocal
167 stimuli with learnt communicative value, dogs were presented with a Meaningful Whistle
168 (test 9). No significant head-turn bias was found (Binomial test: (60% Right head-turn), $p =$
169 0.42), suggesting that the LH advantage for meaningful phonemic content in speech may
170 not extend to other familiar and communicatively relevant non-vocal sounds. Whilst this
171 result may seem in opposition with the LH advantage that characterises the perception of
172 articulated whistled language by experienced human listeners [26], articulated whistled
173 languages encode phonological segmental information [27] and are therefore more
174 comparable to the Meaningful Sine-Wave Speech used in *test 2*, which also triggered a LH

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

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

191 Conclusion

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

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

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

208 **Experimental Procedures**

209 Subjects

210 Subject animals were over six months old, healthy with no known hearing or sight problems
211 and not aggressive towards people. Owners of dogs exposed to the English speech
212 confirmed that their dog responded to the command 'come on then' or a similar variant.
213 Owners of dogs exposed to whistles confirmed that they regularly whistled to call their dog
214 and chose a comparable whistle from the available stimuli. Only dogs with no previous
215 exposure to French were presented with Meaningless (Foreign) Speech with Neutralised
216 Intonation or Meaningful Speech in an Unfamiliar Accent with Neutralised Intonation. An a
217 priori power analysis conducted using G*Power [29] with power ($1 - \beta$) set at 0.80 and $\alpha =$
218 0.05, two-tailed, showed that a minimum sample size of $N = 20$ was required in each
219 condition for detecting a medium sized effect in a binomial test. We included the first 25

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

226 Apparatus

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

234 Procedure

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

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

246 **Supplemental Information**

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

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323

324 Figure Legends

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

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

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

333