



Supplementary Materials for

Neural mechanisms for lexical processing in dogs

A. Andics,* A. Gábor, M. Gácsi, T. Faragó, D. Szabó, Á. Miklósi

*Corresponding author. Email: attila.andics@gmail.com

Published 30 August 2016 on *Science* First Release
DOI: 10.1126/science.aaf3777

This PDF file includes:

Materials and Methods
Fig. S1
Tables S1 to S4
Full Reference List

Materials and Methods

Participants

Thirteen family dogs, living with their owners, were tested (4 breeds: 6 border collies, 5 golden retrievers, 1 German shepherd and 1 Chinese crested; aged 1-12 years (mean = 5, SD = 2.83); 7 females and 6 males). Dog owners volunteered to participate in the training and testing process with their dogs, gave written informed consent and received no monetary compensation. Experimental procedures met the national and European guidelines for animal care and were approved by the local ethical committee (Állatkísérleti Tudományos Etikai Tanács KA-1719, Budapest, Hungary; Pest Megyei Kormányhivatal Élelmiszerlánc-Biztonsági és Állategészségügyi Igazgatósága XIV-I-001/520-4/2012, Budapest, Hungary). The training procedure, developed by MG (19) to prepare dogs for awake fMRI testing was based on conditioning and social learning. Dogs were not restricted in any way and they could leave the scanner any time.

Stimuli

Stimuli were Hungarian words, three with a praise meaning for the dogs (praise words: azaz [ˈɒzɒz] / ügyes [ˈyɟɛʃ] / jól van [ˈjoːlvɒn] for "that's it / clever / well done") and three conjunction words that presumably are not used to address dogs (neutral words: akár [ˈɒkɑːr] / olyan [ˈojɒn] / mégsem [ˈmeːgʃɛm] for "as if / such / yet"). We selected praise words that, based on an open-ended questionnaire, were used by all test dog owners. The term 'neutral' is used here as a synonym for 'meaningless to the dogs' or 'non-praising and not otherwise marked'. All six words were disyllabic, with a matched consonant-vowel structure across praise and neutral words. All six words were recorded with both praising and neutral intonation. We used two tokens per word and per intonation type, adding up to 24 stimuli in total. All stimuli were spoken by a female trainer of the dogs (MG) who was also always present during the test sessions, and talked to the dogs during test preparations, but was never visible to the dogs during the actual test. To increase naturalness, stimuli were recorded as being told to a dog present in the recording room. Stimuli were digitized at a 16 bit/44.1 kHz sampling rate and were equalized for -26 dB RMS using Adobe Audition CS5.5.

Fundamental frequency parameters of the stimulus voice were compared across conditions, using a multivariate ANOVA with fixed factors lexical markedness and intonational markedness. Stimuli with a praising intonation were higher-pitched and had a greater pitch range than stimuli with a neutral intonation (praising / neutral intonation: mean(F0) = 268(±20) / 165(±6) Hz, $F_{1,20} = 289.725$, $p < 0.001$; mean(F0 range) = 277(±93) / 46(±9) Hz, $F_{1,20} = 68.264$, $p < 0.001$) but no systematic pitch differences were found between praise words and neutral words (all $F_s < 1$) (Fig. 1B). To ensure that acoustic variation in the stimuli was not specific to the stimulus voice, we analyzed recordings of the same words with both intonations from 14 other Hungarian speakers (6 males, 8 females, all familiar with dogs). Pitch parameters for these reference voices (N = 14) were compared across conditions in repeated-measures ANOVAs. For reference voices, just as for the stimulus voice, words with praising intonation were higher-pitched and had a greater pitch range than stimuli with neutral intonation (praising / neutral intonation: mean(F0) = 216(±67) / 161(±55) Hz, $F_{1,13} = 67.122$, $p < 0.001$; mean(F0

range) = 144(±71) / 37(±18) Hz, $F_{1,13} = 44.032$, $p < 0.001$) but, again, no systematic pitch differences were found between praise words and neutral words (all $F_s < 1$).

All stimuli were scored for perceived intonation on a scale of five (1: not at all praising; 5: maximally praising) by 17 foreign listeners who did not speak Hungarian and reported not to understand any of the words. Words with a praising intonation were rated as more praising (mean(words with praising intonation) = 3.826, mean(words with neutral intonation) = 1.828, $F_{1,16} = 87.741$, $p < 0.001$), while there was no difference between words with praising and neutral meanings ($F < 1$), according to a repeated-measures ANOVA on perceived intonation scores.

Design and procedure

Four conditions were used: praise words with praising intonation (Pp), praise words with neutral intonation (Pn), neutral words with praising intonation (Np), neutral words with neutral intonation (Nn)(Fig. 1A). Stimuli were grouped into blocks of three words. Each block contained one token of each of the three words corresponding to the given condition, in a varying order. Here is an example of a stimulus block for each condition (intonation in parentheses). Pp: “azaz (praising) – ügyes (praising) – jól van (praising)”, Pn: “jól van (neutral) – azaz (neutral) – ügyes (neutral)”, Np: “mégsem (praising) – akár (praising) - olyan (praising)”, Nn: “olyan (neutral) – mégsem (neutral) – akár (neutral)”. In total, 48 stimulus blocks were created.

Stimulus blocks were presented in silent gaps between 2 s long volume acquisitions. Silent gaps were 5 s long. Stimulus onset was placed 20 ms after the beginning of the silent gap. Average word length was 642 ms (range 484 - 896 ms), and we placed 20 ms long silence periods between words within a block. Average total stimulus block length was 2.3 s. Stimulus block onset asynchrony was 7 s. Each of the 48 stimulus blocks (12 per condition) was presented exactly once per run. Twelve silent blocks were also added. Consecutive blocks were never from the same type, and all conditions were evenly distributed, but trial order was otherwise random. Every run consisted of 60 stimulus blocks, and two extra scans were added to the end. The total length of a run was approximately 7.5 mins. The experiment consisted of two runs, the order of these was counterbalanced across dogs.

Stimuli were controlled using Matlab (version 9.1) Psychophysics Toolbox 3 (40). During scanning, stimulus presentation and data acquisition were synchronized by a TTL trigger pulse. Stimuli were delivered binaurally via MRI-compatible sound-attenuating headphones that covered the ears of the dogs.

Data acquisition

MRI measurements were performed on a 3 T whole body MR unit at the MR Research Centre of the Semmelweis University Budapest. We used a Philips SENSE Flex Medium coil. We obtained EPI-BOLD fMRI time series from 29 transverse slices covering the whole brain. Spatial resolution was 3.5×3.5×3.5 mm, including a 0.5 mm slice gap. A single-shot gradient-echo planar sequence was used (ascending slice order; acquisition matrix 64×64; TR = 7000 ms, including 2000 ms acquisition and 5000 ms silent gap; TE = 36 ms; flip angle = 90°). Both runs included 62 volumes. We also collected a standard T1-weighted three-dimensional scan using a turbo-field echo (TFE) sequence with 180 slices and 1×1×1 mm spatial resolution, for anatomical reference.

Dogs were trained to lie motionless for the whole duration of the run (they were tested one run per session) without any restraints. Runs with suprathreshold motion (more than 3 mm in any direction or more than 1° rotation in any direction) were discarded. We continued test sessions with each dog until we obtained two successful functional runs, until at most three attempts with each of the two runs, and until at most four attempts in total. The average number of test sessions per dog was 2.62, the proportion of successful first / second / third attempts for a given run was 80 / 16 / 4%, respectively. Overall, twelve out of thirteen dogs completed both runs, and one dog completed only one run during these attempts.

Data analysis

We used MATLAB R2013a (<http://www.mathworks.com/products/matlab/>) and SPM8 (www.fil.ion.ucl.ac.uk/spm) for image preprocessing and analyses (41). First, the functional EPI-BOLD images were realigned. The average of maximal movements per dog was below 1.01 mm for each translation direction, and below 0.02 degree for each rotation direction. The average of maximal movements between two consecutive volume acquisitions per dog was below 0.45 mm for each translation direction, and below 0.01 degree for each rotation direction. Individual translation movements per run, per direction are shown in Figure S1. Second, the structural image of the dog was aligned manually to the template anatomical image (a selected golden retriever, the same as in (19)). Third, the mean functional image was co-registered manually to the structural image, and the resulting transformation matrix was applied to all realigned functional images. The structural image was spatially normalized and transformed via SPM's standard nonlinear warping function with 16 iterations into a common anatomical space (the template). The same dog brain space was used as in (19), with x, y and z coordinates denoting left to right, posterior to anterior, and inferior to superior directions respectively. We then applied the resulting transformation matrix to all co-registered functional images. Finally, normalized functionals were convolved with an isotropic 3-D Gaussian kernel (FWHM = 4 mm) for spatial filtering.

The fMRI data were analyzed using a general linear model and statistical parametric mapping. We constructed three models: one with condition regressors for each run and for each block type: Pp, Pn, Np, Nn and silence; and two with parametric modulators of F0 and F0 change across all conditions (in both orders). As parametric modulators are serially orthogonalised in SPM, parametric effects were calculated for the first parametric modulator in each model. Conditions were modeled as 2.3 s long blocks. Realignment regressors for each run were also included to model potential movement artifacts. To remove low-frequency signals, we used a high-pass filter with a cycle-cutoff of 128 s. Regressors were convolved with the canonical haemodynamic response function of SPM. Single-subject fixed effect analyses were followed by lateralization tests (Table S1), small-volume corrected random effects analyses on the group level (Table S2, S3), and condition-specific seed-to-voxel functional connectivity analyses (Table S4).

To obtain a robust and specific measure of laterality which is not based on a single cutoff threshold, lateralization indices were calculated using a bootstrapping analysis approach as described in (29), and as implemented in SPM's LI-Toolbox (42). Input to this analysis were the subject-specific contrast images for each condition (compared to silence), with an exclusive midline mask of 11 mm. LIs are iteratively calculated at

different thresholds. 20 thresholding intervals are used, defined as equally sized steps from 0 to the maximum value in the masked image (different per subject and per contrast, range 2.1 - 6.5; Fig. 1C). 100 bootstrapped resamples are then generated for each side, from which all 1.000 possible LI combinations are calculated for each threshold, resulting in an overall maximum of 20.000 indices. To increase the stability of the results, this approach uses trimmed mean values when analyzing LIs from each threshold, using only the mean 50% of data for each single iteration, thus providing a more representative measure of the real center of the distribution. To increase the specificity of the results, this approach takes a weighted mean of LIs from all thresholding results, based on the trimmed means obtained at each threshold. Each trimmed mean value is weighted by its respective threshold, therefore voxels with a higher contrast value get a higher weight. The process resulted in an overall weighted bootstrapped LI per subject and per contrast. These LIs across subjects and conditions were then compared in one-sample T-tests to assess condition-specific hemispheric bias, and in repeated-measures ANOVAs with lexical and intonational markedness as factors (Fig. 1C, Table S1). LIs were also calculated for frontal, temporal, parietal and occipital lobes separately, but no significant effects or tendencies were found in either test (all p s > 0.1). LIs were also calculated for the human non-speech vocalizations vs. silence contrast from a previous study (19), and showed no significant hemisphere bias (mean(LI) = 0.060(\pm 0.330), $T(12) = 0.603$, $p = 0.560$).

For small-volume corrected random effects tests, brain search space was narrowed down to auditory regions and to primary reward regions. For auditory regions, we used a functionally determined mask (Fig. 1D, Table S2). This auditory mask involved the bilateral auditory cortex, extending from close-to-primary, middle ectosylvian regions to caudal and rostral ectosylvian gyrus and to the suprasylvian sulcus; two further cortical clusters in the left caudal and right middle ectosylvian gyri; and two subcortical clusters in the tectum mesencephali, near the bilateral inferior colliculi. For primary reward regions, anatomical masks were used. VTA-SN and VS were determined manually on the template brain (VTA-SN: 50 voxels, R VS: 109 voxels, L VS: 100 voxels), using anatomical atlas (30) for reference. VTA-SN is between the cerebral crura's caudo-rostral split on the basal surface of the mesencephalon and the mammillary body, directly above the surface of the interpeduncular fossa. The extent of A9 and 10 dopaminergic nuclei that constitute SN's pars compacta and the VTA is on the scale of several mm-s in each dimension. On MR anatomical images, they are indistinguishable from the interpeduncular nucleus. VS includes the nucleus accumbens, and more dorsally the caudate nucleus and the putamen (24). All regional tests are reported in Table S3. A follow-up regional test in R mESG's left homologue (L mESG) was also performed: no intonational effect or F0 effect was found, but also no significant difference across hemispheres (hemisphere \times intonation: $F_{1,12} = 1.556$, $p = 0.236$; F0: mean(L-R) = 0.003(\pm 0.011), $T(12) = 1.167$, $p = 0.266$).

For functional connectivity analyses, we applied a seed-to-voxel approach as implemented in SPM's CONN toolbox (43). Auditory mask subregions were used as seeds. Condition-specific connectivity scores (Fisher-transformed correlation coefficients) were contrasted in random effects tests. Effects are reported on the whole-brain level in Table S4.

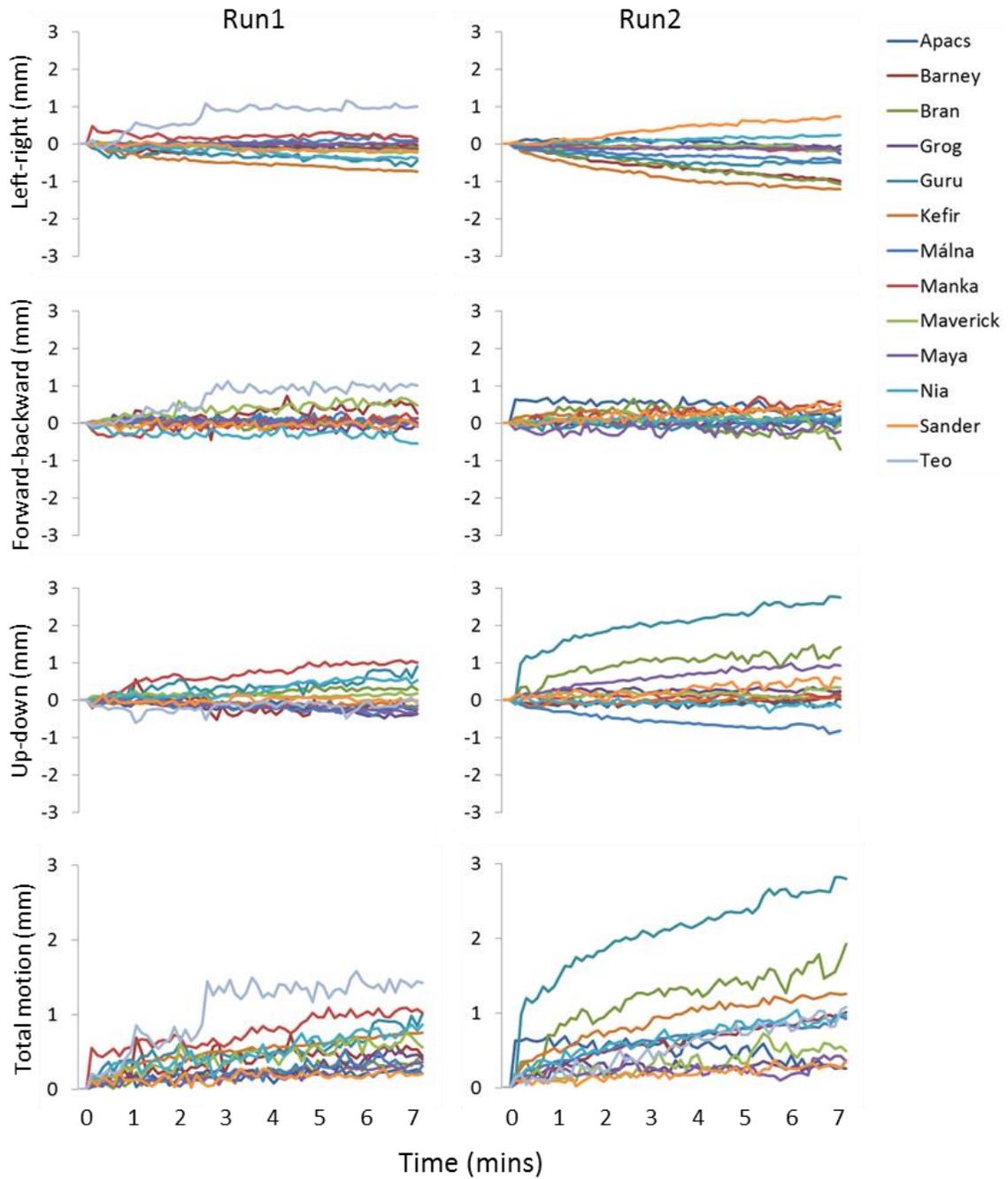


Fig. S1.

Individual dog movement parameters. Lines represent individual motion parameters for each translation direction (x axis: left-right, y axis: forward-backward, z axis: up-down) during 7 mins functional runs. Total motion refers to the Euclidean distance from the start position, calculated as the square root of $x^2 + y^2 + z^2$.

Table S1.

Overall lateralization effects across conditions and thresholding steps. Positive values denote LH bias. Effects surviving a $p < 0.05$ significance threshold are in bold. LEX: lexical, INT: intonational.

	Pp	Pn	Np	Nn	LEX	INT	LEX × INT
Overall LI (mean)	0.210	0.284	0.161	0.116			
95% CI	0.026- 0.395	0.118- 0.449	-0.017- 0.339	-0.074- 0.307			
T(12)	2.480	3.730	1.970	1.330			
F(1,12)					6.360	0.052	1.227
p	0.029	0.003	0.073	0.209	0.027	0.823	0.290
p (per thresholding step)							
1	0.003	0.001	0.080	0.060	0.005	0.824	0.968
2	0.006	0.001	0.098	0.071	0.009	0.954	0.942
3	0.012	0.001	0.137	0.110	0.009	0.916	0.776
4	0.017	0.001	0.193	0.160	0.009	0.824	0.695
5	0.020	0.001	0.253	0.209	0.009	0.722	0.615
6	0.021	0.001	0.342	0.275	0.007	0.748	0.634
7	0.028	0.000	0.414	0.318	0.008	0.670	0.609
8	0.033	0.000	0.448	0.402	0.008	0.639	0.531
9	0.038	0.000	0.424	0.421	0.007	0.616	0.463
10	0.039	0.001	0.403	0.373	0.007	0.587	0.480
11	0.042	0.001	0.304	0.324	0.007	0.557	0.410
12	0.038	0.001	0.249	0.276	0.006	0.541	0.384
13	0.029	0.001	0.153	0.201	0.007	0.522	0.304
14	0.022	0.001	0.083	0.180	0.008	0.551	0.197
15	0.017	0.001	0.039	0.158	0.017	0.733	0.177
16	0.011	0.002	0.023	0.120	0.027	0.927	0.260
17	0.010	0.002	0.021	0.102	0.030	0.985	0.341
18	0.010	0.002	0.018	0.088	0.052	0.934	0.444
19	0.018	0.004	0.020	0.078	0.098	0.992	0.517
20	0.021	0.018	0.034	0.085	0.149	0.985	0.815

Table S2.

Auditory regions responsive to speech. The table lists a single peak per cluster for the speech (Pp+Pn+Np+Nm) > silence contrast, voxel threshold $p < 0.001$, clusters of min. 5 voxels. These voxels constituted the auditory mask.

Brain region	x	y	z	T(12)	vol (mm³)	p
Left middle suprasylvian sulcus (L mSSS)	-18	-14	14	6.06	1288	< 0.001
Right middle ectosylvian sulcus (R mESS)	28	-10	8	7.90	1272	< 0.001
Left caudal ectosylvian gyrus (L cESG)	-26	-10	-6	6.49	232	< 0.001
Right middle ectosylvian gyrus (R mESG)	22	2	14	5.30	64	< 0.001
Left tectum mesencephali (L TM)	-2	-12	-10	4.84	64	< 0.001
Right tectum mesencephali (R TM)	4	-8	-12	4.78	48	< 0.001

Table S3.

Random effects tests of lexical and intonational processing, and of acoustic parameters. An overall voxel threshold $p < 0.0005$ was applied. Only clusters FWE cluster-corrected for multiple comparisons across the corresponding small volume (in parentheses) are reported ($p_{SVC} < 0.05$). All clusters had a single peak. n.s.: no significant clusters.

Contrast	Brain region	x	y	z	T(12)	p	p _{SVC}
Lexical							
Pp+Pn > Np+Nn	n.s.						
Pp+Pn < Np+Nn	n.s.						
Intonational							
Pp+Np > Pn+Nn	n.s.						
Pn+Nn < Pp+Np	R mESG	20	0	18	4.34	< 0.0005	0.041 (aud. mask)
Lexical and intonational							
Pp+Nn > Pn+Np	VTA-SN	-4	-18	-20	4.53	< 0.0005	0.009 (VTA-SN)
Pp > Pn+Np+Nn	VTA-SN	2	-16	-20	4.67	< 0.0005	0.007 (VTA-SN)
	R CN	2	10	6	5.50	< 0.0005	0.022 (R VS)
	L CN	-6	10	4	4.29	< 0.0005	0.022 (L VS)
(Pp > Pn)∩(Pp > Np)	VTA-SN	-4	-16	-22	4.76	< 0.0005	0.005 (VTA-SN)
	R CN	6	12	6	4.64	< 0.0005	0.055 (R VS)
	L CN	-10	2	6	4.48	< 0.0005	0.039 (L VS)
F0 (parametric)							
positive	n.s.						
negative	R mESG	22	2	14	4.53	< 0.0005	0.040 (aud. mask)
F0 change (parametric)							
positive	n.s.						
negative	n.s.						

Table S4.

Seed-to-voxel functional connectivity tests. An overall voxel threshold $p < 0.0005$ was applied. Only peaks FWE corrected for the whole brain are reported ($p_{WBC} < 0.05$). n.s.: no significant clusters for any seed region.

Contrast	Seed region	Brain region	x	y	z	T(12)	p	p_{WBC}
Lexical								
$Pp+Pn > Np+Nn$	<i>n.s.</i>							
$Pp+Pn < Np+Nn$	<i>n.s.</i>							
Intonational								
$Pp+Np > Pn+Nn$	R mESG	R CN	4	10	0	8.99	<0.0005	0.046
$Pp+Np < Pn+Nn$	<i>n.s.</i>							
Lexical and intonational								
$Pp+Nn > Pn+Np$	<i>n.s.</i>							
$Pp > Pn+Np+Nn$	<i>n.s.</i>							
$(Pp > Pn) \cap (Pp > Np)$	<i>n.s.</i>							

References and Notes

1. E. F. Briefer, Vocal expression of emotions in mammals: Mechanisms of production and evidence. *J. Zool.* **288**, 1–20 (2012). [doi:10.1111/j.1469-7998.2012.00920.x](https://doi.org/10.1111/j.1469-7998.2012.00920.x)
2. S. Frühholz, W. Trost, S. A. Kotz, The sound of emotions—Towards a unifying neural network perspective of affective sound processing. *Neurosci. Biobehav. Rev.* **68**, 96–110 (2016). [Medline doi:10.1016/j.neubiorev.2016.05.002](https://doi.org/10.1016/j.neubiorev.2016.05.002)
3. M. J. Yip, The search for phonology in other species. *Trends Cogn. Sci.* **10**, 442–446 (2006). [Medline doi:10.1016/j.tics.2006.08.001](https://doi.org/10.1016/j.tics.2006.08.001)
4. K. Collier, B. Bickel, C. P. van Schaik, M. B. Manser, S. W. Townsend, Language evolution: Syntax before phonology? *Proc. R. Soc. B Biol. Sci.* **281**, 20140263 (2014).
5. R. M. Seyfarth, D. L. Cheney, P. Marler, Monkey responses to three different alarm calls: Evidence of predator classification and semantic communication. *Science* **210**, 801–803 (1980). [Medline doi:10.1126/science.7433999](https://doi.org/10.1126/science.7433999)
6. I. M. Pepperberg, H. R. Shive, Simultaneous development of vocal and physical object combinations by a grey parrot (*Psittacus erithacus*): Bottle caps, lids, and labels. *J. Comp. Psychol.* **115**, 376–384 (2001). [Medline doi:10.1037/0735-7036.115.4.376](https://doi.org/10.1037/0735-7036.115.4.376)
7. J. R. Binder, R. H. Desai, W. W. Graves, L. L. Conant, Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cereb. Cortex* **19**, 2767–2796 (2009). [Medline doi:10.1093/cercor/bhp055](https://doi.org/10.1093/cercor/bhp055)
8. D. Poeppel, The analysis of speech in different temporal integration windows: Cerebral lateralization as “asymmetric sampling in time”. *Speech Commun.* **41**, 245–255 (2003). [doi:10.1016/S0167-6393\(02\)00107-3](https://doi.org/10.1016/S0167-6393(02)00107-3)
9. W. Wetzel, F. W. Ohl, H. Scheich, Global versus local processing of frequency-modulated tones in gerbils: An animal model of lateralized auditory cortex functions. *Proc. Natl. Acad. Sci. U.S.A.* **105**, 6753–6758 (2008). [Medline doi:10.1073/pnas.0707844105](https://doi.org/10.1073/pnas.0707844105)
10. Y. Shtyrov, E. Pihko, F. Pulvermüller, Determinants of dominance: Is language laterality explained by physical or linguistic features of speech? *Neuroimage* **27**, 37–47 (2005). [Medline doi:10.1016/j.neuroimage.2005.02.003](https://doi.org/10.1016/j.neuroimage.2005.02.003)
11. A. Poremba, M. Malloy, R. C. Saunders, R. E. Carson, P. Herscovitch, M. Mishkin, Species-specific calls evoke asymmetric activity in the monkey’s temporal poles. *Nature* **427**, 448–451 (2004). [Medline doi:10.1038/nature02268](https://doi.org/10.1038/nature02268)
12. G. Ehret, Left hemisphere advantage in the mouse brain for recognizing ultrasonic communication calls. *Nature* **325**, 249–251 (1987). [Medline doi:10.1038/325249a0](https://doi.org/10.1038/325249a0)
13. H. U. Voss, K. Tabelow, J. Polzehl, O. Tchernichovski, K. K. Maul, D. Salgado-Commissariat, D. Ballon, S. A. Helekar, Functional MRI of the zebra finch brain during song stimulation suggests a lateralized response topography. *Proc. Natl. Acad. Sci. U.S.A.* **104**, 10667–10672 (2007). [Medline doi:10.1073/pnas.0611515104](https://doi.org/10.1073/pnas.0611515104)
14. P. Pongrácz, C. Molnár, A. Miklósi, Barking in family dogs: An ethological approach. *Vet. J.* **183**, 141–147 (2010). [Medline doi:10.1016/j.tvjl.2008.12.010](https://doi.org/10.1016/j.tvjl.2008.12.010)

15. J. M. Gibson, S. A. Scavelli, C. J. Udell, M. A. R. Udell, Domestic dogs (*Canis lupus familiaris*) are sensitive to the “human” qualities of vocal commands. *Anim. Behav. Cogn.* **1**, 281–295 (2014). [doi:10.12966/abc.08.05.2014](https://doi.org/10.12966/abc.08.05.2014)
16. Á. Miklósi, J. Topál, V. Csányi, Comparative social cognition: What can dogs teach us? *Anim. Behav.* **67**, 995–1004 (2004). [doi:10.1016/j.anbehav.2003.10.008](https://doi.org/10.1016/j.anbehav.2003.10.008)
17. J. Topál, G. Gergely, A. Erdőhegyi, G. Csibra, A. Miklósi, Differential sensitivity to human communication in dogs, wolves, and human infants. *Science* **325**, 1269–1272 (2009). [Medline](https://pubmed.ncbi.nlm.nih.gov/1176960/) [doi:10.1126/science.1176960](https://doi.org/10.1126/science.1176960)
18. J. Kaminski, J. Call, J. Fischer, Word learning in a domestic dog: Evidence for “fast mapping”. *Science* **304**, 1682–1683 (2004). [Medline](https://pubmed.ncbi.nlm.nih.gov/1097859/) [doi:10.1126/science.1097859](https://doi.org/10.1126/science.1097859)
19. A. Andics, M. Gácsi, T. Faragó, A. Kis, A. Miklósi, Voice-sensitive regions in the dog and human brain are revealed by comparative fMRI. *Curr. Biol.* **24**, 574–578 (2014). [Medline](https://pubmed.ncbi.nlm.nih.gov/2491058/) [doi:10.1016/j.cub.2014.01.058](https://doi.org/10.1016/j.cub.2014.01.058)
20. V. F. Ratcliffe, D. Reby, Orienting asymmetries in dogs’ responses to different communicatory components of human speech. *Curr. Biol.* **24**, 2908–2912 (2014). [Medline](https://pubmed.ncbi.nlm.nih.gov/2491030/) [doi:10.1016/j.cub.2014.10.030](https://doi.org/10.1016/j.cub.2014.10.030)
21. A. Fernald, Intonation and communicative intent in mothers’ speech to infants: Is the melody the message? *Child Dev.* **60**, 1497–1510 (1989). [Medline](https://pubmed.ncbi.nlm.nih.gov/1130938/) [doi:10.2307/1130938](https://doi.org/10.2307/1130938)
22. W. Schultz, P. Dayan, P. R. Montague, A neural substrate of prediction and reward. *Science* **275**, 1593–1599 (1997). [Medline](https://pubmed.ncbi.nlm.nih.gov/53061593/) [doi:10.1126/science.275.5306.1593](https://doi.org/10.1126/science.275.5306.1593)
23. J. P. O’Doherty, Reward representations and reward-related learning in the human brain: Insights from neuroimaging. *Curr. Opin. Neurobiol.* **14**, 769–776 (2004). [Medline](https://pubmed.ncbi.nlm.nih.gov/10016016/) [doi:10.1016/j.conb.2004.10.016](https://doi.org/10.1016/j.conb.2004.10.016)
24. S. N. Haber, B. Knutson, The reward circuit: Linking primate anatomy and human imaging. *Neuropsychopharmacology* **35**, 4–26 (2010). [Medline](https://pubmed.ncbi.nlm.nih.gov/101038129/) [doi:10.1038/npp.2009.129](https://doi.org/10.1038/npp.2009.129)
25. S. J. Russo, E. J. Nestler, The brain reward circuitry in mood disorders. *Nat. Rev. Neurosci.* **14**, 609–625 (2013). [Medline](https://pubmed.ncbi.nlm.nih.gov/1010383381/) [doi:10.1038/nrn3381](https://doi.org/10.1038/nrn3381)
26. G. S. Berns, A. Brooks, M. Spivak, Replicability and heterogeneity of awake unrestrained canine fMRI responses. *PLOS ONE* **8**, e81698 (2013). [Medline](https://pubmed.ncbi.nlm.nih.gov/0081698/) [doi:10.1371/journal.pone.0081698](https://doi.org/10.1371/journal.pone.0081698)
27. A. Kerepesi, A. Dóka, Á. Miklósi, Dogs and their human companions: The effect of familiarity on dog-human interactions. *Behav. Processes* **110**, 27–36 (2015). [Medline](https://pubmed.ncbi.nlm.nih.gov/201402005/) [doi:10.1016/j.beproc.2014.02.005](https://doi.org/10.1016/j.beproc.2014.02.005)
28. Materials and methods are available as supplementary materials on *Science Online*.
29. M. Wilke, V. J. Schmithorst, A combined bootstrap/histogram analysis approach for computing a lateralization index from neuroimaging data. *Neuroimage* **33**, 522–530 (2006). [Medline](https://pubmed.ncbi.nlm.nih.gov/200607010/) [doi:10.1016/j.neuroimage.2006.07.010](https://doi.org/10.1016/j.neuroimage.2006.07.010)
30. H. E. Evans, A. de Lahunta, *Miller’s Anatomy of the Dog* (Saunders-Elsevier, ed. 4, 2013).
31. S. Norman-Haignere, N. Kanwisher, J. H. McDermott, Cortical pitch regions in humans respond primarily to resolved harmonics and are located in specific tonotopic regions of

- anterior auditory cortex. *J. Neurosci.* **33**, 19451–19469 (2013). [Medline doi:10.1523/JNEUROSCI.2880-13.2013](#)
32. D. Bendor, X. Wang, The neuronal representation of pitch in primate auditory cortex. *Nature* **436**, 1161–1165 (2005). [Medline doi:10.1038/nature03867](#)
33. D. Wildgruber, H. Ackermann, B. Kreifelts, T. Ethofer, Cerebral processing of linguistic and emotional prosody: fMRI studies. *Prog. Brain Res.* **156**, 249–268 (2006). [Medline doi:10.1016/S0079-6123\(06\)56013-3](#)
34. V. N. Salimpoor, I. van den Bosch, N. Kovacevic, A. R. McIntosh, A. Dagher, R. J. Zatorre, Interactions between the nucleus accumbens and auditory cortices predict music reward value. *Science* **340**, 216–219 (2013). [Medline doi:10.1126/science.1231059](#)
35. D. A. Sauter, F. Eisner, P. Ekman, S. K. Scott, Cross-cultural recognition of basic emotions through nonverbal emotional vocalizations. *Proc. Natl. Acad. Sci. U.S.A.* **107**, 2408–2412 (2010). [Medline doi:10.1073/pnas.0908239106](#)
36. T. Faragó, A. Andics, V. Devecseri, A. Kis, M. Gácsi, A. Miklósi, Humans rely on the same rules to assess emotional valence and intensity in conspecific and dog vocalizations. *Biol. Lett.* **10**, 20130926 (2014). [Medline doi:10.1098/rsbl.2013.0926](#)
37. P. Belin, S. Fecteau, I. Charest, N. Nicastró, M. D. Hauser, J. L. Armony, Human cerebral response to animal affective vocalizations. *Proc. R. Soc. B Biol. Sci.* **275**, 473–481 (2008).
38. S. A. Kotz, S. Paulmann, Emotion, language, and the brain. *Lang. Linguist. Compass* **5**, 108–125 (2011). [doi:10.1111/j.1749-818X.2010.00267.x](#)
39. M. C. Corballis, Left brain, right brain: Facts and fantasies. *PLOS Biol.* **12**, e1001767 (2014). [Medline doi:10.1371/journal.pbio.1001767](#)
40. M. Kleiner, D. Brainard, D. Pelli, A. Ingling, What's new in Psychtoolbox-3. *Perception* **36**, 1–16 (2007).
41. K. J. Friston, J. T. Ashburner, S. J. Kiebel, T. E. Nichols, W. D. Penny, *Statistical Parametric Mapping: The Analysis of Functional Brain Images* (Elsevier, 2007).
42. M. Wilke, K. Lidzba, LI-tool: A new toolbox to assess lateralization in functional MR-data. *J. Neurosci. Methods* **163**, 128–136 (2007). [Medline doi:10.1016/j.jneumeth.2007.01.026](#)
43. S. Whitfield-Gabrieli, A. Nieto-Castanon, Conn: A functional connectivity toolbox for correlated and anticorrelated brain networks. *Brain Connect.* **2**, 125–141 (2012). [Medline doi:10.1089/brain.2012.0073](#)