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A left-lateralized white matter tract associated with communication in domestic dogs

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The ability to communicate with conspecifics is an adaptive behavior important for survival and reproduction, particularly in lineages that evolved enlarged brains and complex social behavior. In humans, language is supported by a robust, left-lateralized white matter fiber tract called the arcuate fasciculus, which links Broca's and Wernicke's areas, the core neocortical language regions located in the frontal and temporal lobes, respectively[1]. This tract is also present in chimpanzees, less substantial than in humans and either weakly leftwardly-asymmetric or not asymmetric[2]. Other mammalian lineages have evolved large brains, complex behavior and social communication in parallel with primates, notably including carnivores. In dogs (*Canis familiaris*), domestication has almost certainly involved additional selective pressures and environmental factors that have shaped the evolution and development of neural circuits for communication. We report that the dog brain possesses a large, left-lateralized white matter tract that links cortical centers for productive and receptive communication, and that this tract is positively associated with individual variation in receptive vocabulary size.

Neuroimaging data were acquired non-invasively from 107 dogs (mean age 3.2 +/- 2.2 years; 66 female; 16 breeds/types). Dogs were working dogs and/or companion animals in the households of members of the general population across the United States. All owners provided informed consent and study procedures were approved by the IACUC and IRB at Harvard University. Scans included 60-direction DWI images (1.30 mm^3, 2 averages with reversed phase encoding, 12 B0s) and T1-weighted images (0.67 mm^3, 2 averages). The FSL software package was used for preprocessing and probabilistic tractography.

We examined connectivity between cortical regions that contribute to productive and receptive communication. The precruciate gyrus (XC) is a vocal premotor region that exerts direct control on the laryngeal muscles and is responsive to spoken familiar human language[3]. In the temporal lobe, we examined connections linking XC to the caudal ectosylvian gyrus (cESG), an auditory association region consistently implicated in awake dog fMRI studies in the comprehension of auditory information, voice identity processing, and emotional valence processing, and the rostral ectosylvian gyrus (rESG), a secondary auditory region which also responds to human spoken language[3–5]. Direct, monosynaptic connections between these frontal and temporal regions have previously been identified in tract-tracing studies[6,7], but whether these connections resolve into a coherent tract, whether they are asymmetric, and how they relate to behavior are all currently unknown. We carried out bidirectional tractography between each frontal–temporal region pair. Tracts were thresholded at 0.1% of the tractography waytotal. For each tract in each dog, we measured tract volume and asymmetry quotient, defined as: AQ = (R – L) / [(R + L) x 0.5]. In order to prevent measurement of connections beyond the core of the tract body, we constrained volume and asymmetry measurements to above-threshold connectivity within a tract archetype mask.

Additionally, owners provided a list of all words to which their dogs reliably responded in an accurate manner in everyday life, which we consider to be an imperfect but moderately accurate representation of dogs' actual receptive vocabulary size. The current results suggest the existence of a meaningful brain–behavior relationship but should be followed up with future research using a more direct assessment of canine communication abilities.

XC-rESG and XC-cESG connections substantially overlapped, indicating that this is a single fronto-temporal fiber system with branching terminations in the temporal lobe. The human arcuate fasciculus also displays this morphology. Figure 1 shows both measured components of this tract, their asymmetry quotients, and their relationship to owner-reported

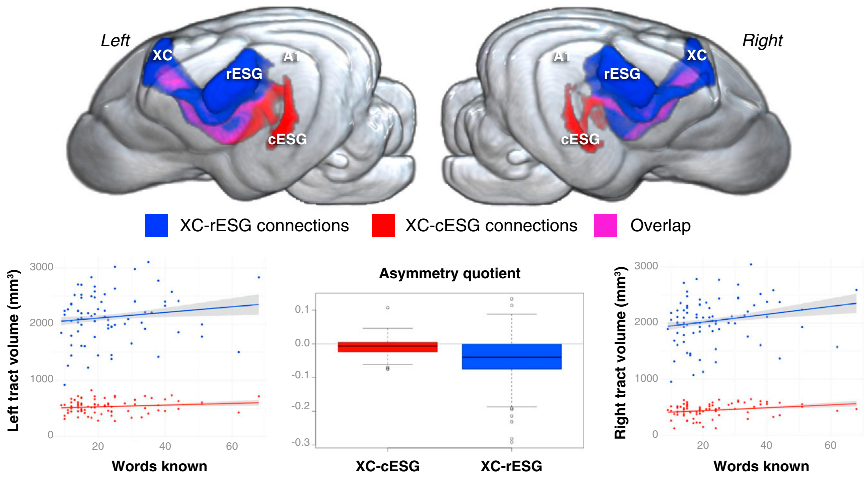

Figure 1. A left-lateralized white matter tract associated with communication in domestic dogs.
A leftwardly-asymmetric tract connects the premotor center for vocal motor production (XC) to temporal centers for receptive communication (rESG and cESG) and predicts receptive vocabulary size across dogs. The location of primary auditory cortex is also marked (A1). Image illustrates above-threshold tractography in both the XC-rESG and XC-cESG connections in at least 67.7% of the 106-dog sample.

receptive vocabulary size. XC-rESG connections are more uniformly robust across individuals, while XC-cESG connections show more variability. Both the rostral and caudal components of the tract were significantly larger in the left hemisphere (XC-cESG: $t(106) = -5.9051$, $p < 0.0001$; XC-rESG: $t(106) = -3.5243$, $p = 0.0006$). Furthermore, components of this tract were significantly associated with owner-reported receptive vocabulary size in both the left and right hemispheres (left XC-cESG: $\beta = 1.588$, $\chi^2(1) = 1.9892$, $p = 0.1584$; right XC-cESG: $\beta = 2.566$, $\chi^2(1) = 5.3586$, $p = 0.0206$; left XC-rESG: $\beta = 9.546$, $\chi^2(1) = 6.6517$, $p = 0.0099$; right XC-rESG: $\beta = 10.410$, $\chi^2(1) = 8.7373$, $p = 0.0031$).

Together, these results indicate that, in dogs, premotor vocal production cortex is robustly connected to temporal perceptual communication cortex through a coherent, myelinated white matter tract. Further, this connectivity is leftwardly-asymmetric and associated with communication behavior in both hemispheres, paralleling the anatomy and function of the human arcuate fasciculus, which is larger in the left hemisphere but implicated in language processing in both hemispheres, although it is important to note that lateralization in animals does not always parallel human patterns[8]. Notably, the phylogenic lineages of carnivores (dogs) and primates (humans) are separated by approximately 95 million years of divergent evolution, and their last common ancestor had a relatively small brain with a simple neocortical mantle consisting mostly of primary sensory and motor regions[9]. Larger brains and expanded neocortical association regions evolved independently in carnivores and primates, including the independent expansion of temporal cortex into a lobular structure, and the independent enlargement of prefrontal cortex[10].

Why might this pattern exist in such distantly-separated species whose brains have enlarged and elaborated so independently for so long? Dense, myelinated fiber bundles allow rapid information transfer between distant brain regions, which is clearly necessary to integrate vocal motor production and perceptual processing in human communication, which is marked by turn-taking and vocal learning. However, dogs are not generally considered vocal learners. One possibility is that some early placental mammals possessed some degree of connectivity between the ancestral homologs of extant primate and carnivore frontal and temporal communication regions. If this is the case, then comparable connections are likely to exist in most or all living mammals. In potential alignment with this idea, behavioral left-lateralization of communication functions has been observed in many species, including non-mammals[8].

Importantly, though, even humans' closest living ape relatives, chimpanzees, have an arcuate fasciculus that does not show clear signs of leftward asymmetry at the population level. Speculatively, this raises the possibility that selection pressures unique to the human socio-communicative niche, in which dogs and humans are both embedded, may have driven the accumulation of heritable traits promoting the enlargement and leftward-asymmetry of these tracts in both species. Direct comparisons with wild canids would be necessary to confirm this possibility. Alternatively or in combination, early developmental over-proliferation of axonal connections might produce initial, transient, dense connectivity between these regions — which is then substantially pruned in most species but is maintained into adulthood in dogs and humans. Within this potential scenario, it may be shared immersion in a language-rich environment, rather than or in addition to shared evolved anatomical adaptation, which produces a robust, left-lateralized, prefrontal–temporal vocal communication network in the brains of both dogs and humans. The heritable and experience-dependent traits driving the anatomy of these connections in dogs are an important topic for future research.

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AUTHOR CONTRIBUTIONS

S.B. and E.H. collected data; I.L., M.S. and E.H. analysed data; I.L. and E.H. wrote the paper; S.B. and M.S. edited the paper.

DECLARATION OF INTERESTS

The authors declare no competing interests.

SUPPLEMENTAL INFORMATION

Supplemental information including one figure with masks and tracts, one table with subject details, supplemental experimental procedures, and supplemental statistical analyses can be found with this article online at https://doi.org/10.1016/j.cub.2024.09.021.

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