

Say What? The Neuroanatomy of Language Organisation

Language processing was initially posited to be organized into two distinct areas concerned with motor and sensory language function respectively. Broca's area; located in the posterior inferior frontal gyrus (pIFG), is involved in speech production. Whilst Wernicke's area; located in the superior temporal gyrus (STG), is involved in auditory language comprehension. These sites are connected subcortically via the arcuate fasciculus (AF) fibre tract. This connection allows for auditory-motor interactions (Chang et al. 2015). This classic model has been extended to the consensus that there is a left-hemispheric, continuous perisylvian region which is language specific and spans from insular regions and areas of the sensorimotor cortex, connecting the frontal, temporal and some of the inferior parietal lobe. Changes in blood flow due to language activation, as seen in PET studies, are mainly exhibited in this left-hemispheric perisylvian zone (Habib & Demonet, 1996). Right-hemispheric homologues have also been found for these regions, although most people (96% of right-handers, and 70% of left-handers) exhibit a left hemisphere dominance (Lurito & Dziedzic, 2001).

The classic model was built on the interaction of the following brain regions. Broca's area was the first language-specific localized area discovered. It is situated in the pIFG in Brodmann's areas BA44 and BA45. Broca's area is involved in speech production, covert speech planning, and the performance of complex sequences with the hands. The area is activated even when solely observing another human performing these movements (Rizzolatti & Arbib, 1998). The area is heavily rooted in the protomotor formulation of communication as evidenced by its activation in silent speech and mouth movements in PET studies (Habib & Demonet, 1996; Bates & Dick, 2000). Broca's area is also thought to play a role in lexical-semantic processing, which involves the interpretation of the meaning and vocabulary of associated words as demonstrated by fMRI (Binder et al. 1997). Wernicke's area is located in the posterior temporal region which corresponds to BA22, it is thus caudal and inferior to the primary and secondary auditory cortices (Habib & Demonet, 1996). It is responsible for speech comprehension, and receptive phonological processing along with the neighbouring inferior parietal area BA 40 (Binder et al. 1997; Castillo et al. 2001). There is some debate regarding the specific speech comprehension functions of Wernicke's area, Mesulam (1990) believes that it acts solely as the gateway to an interconnected grid which contains relevant areas for interpreting sound meaning relationships. The arcuate fasciculus is the final component of the classic model of language organization. It is a subcortical white-matter fibre tract which connects the pIFG to the STG. DT-MRI tractography illustrated this direct pathway connecting the temporal and frontal regions, this pathway is responsible for phonological processes, such as automatic repetition (Catani et al. 2005). The AF is part of the dorsal stream of language processing (Chang et al. 2015), which is fundamental for language functioning, and specifically the ability to process complex sentence structures (Friederici, 2009).

It is now known that language functioning is distributed widely throughout the brain. The classic model was developed relying almost exclusively on insight from lesion studies, advances in experimental and neuroimaging techniques have revealed a much wider distribution of language-specific functioning. This network includes prefrontal and parietal regions; basal, medial and ventral temporal areas, areas of the occipital cortex, as well as subcortical findings (Bates & Dick, 2000). Using DTI Tractography, Glasser and Rilling (2008) found evidence in support of the language model proposed by Hickok and Poeppel (2004) and the definition of Wernicke's area given by Mesulam (1990). This model posits that incoming auditory information is first processed in the auditory cortex, from there it undergoes phonological decoding in Wernicke's area, where it can then proceed to Broca's area via the AF if immediate repetition is required; or it can proceed to the cortex below the superior temporal sulcus (STS) to undergo lexical and semantic evaluation. This network-based model is built on parallel streams of processing which take place in cortical and subcortical areas. The pathways delineate dorsally and ventrally. The dorsal stream, which runs from the posterosuperior temporal to inferior frontal cortices, is responsible for phonological processing and sensorimotor integration (Friederici, 2009). The superior longitudinal fasciculus and the AF are involved in the dorsal stream. Whilst the ventral stream, which relays information from the temporal pole to the basal occipitotemporal cortex, is responsible for semantic processing (Chang et al. 2015). Using diffusion MRI tractography, Parker et al., (2005) found evidence for a left-hemispheric, second ventral pathway connecting Wernicke's and Broca's areas.

Other brain areas involved in the dual stream model include the middle temporal gyrus (MTG). Howard et al. (1992) found the MTG to be the focus of posterior temporal activation in a study utilizing visual

stimuli. Direct cortical stimulation studies also illustrate the MTG's involvement in auditory comprehension, and that of a much larger network encompassing much of the superior temporal and the inferior frontal lobes. Furthermore, when contrasted with a resting baseline, listening to speech activates the STG bilaterally including the dorsal STG and superior temporal sulcus (STS) (Hickok, 2012). Parts of the STS are also activated by speech production, as well as, speech perception in the left hemisphere as evidenced by fMRI (Narain et al. 2003). The thalamus likely plays a role in language processing also, as patients suffering from decreased perfusion from the thalamic hemisphere often exhibit mutism, initiation deficits, dysnomia and paraphasias (Jonas, 1982). Similarly, the basal ganglia, is another subcortical structure which likely participates in language processing. It is debated whether it is involved in the coordination of timing cues in speech, inhibiting redundant aspects of the language plan or via the application of grammatical components to language (Chang et al. 2005; Crosson, 1985). The occipital cortex also plays its role in language processing. The visual word form area (VWFA) is part of the left ventral stream and identifies visual words, the reading system develops in the lateral occipitotemporal sulcus. However, there is debate as to the origins of word recognition as fMRI studies, like that of Szwed et al., (2011), suggest that it begins prior to the VWFA in the occipital cortex. Demonet et al. (2005) also note that some researchers have found evidence that the left basal temporal area, the opercular frontal cortex and the left anterior insular cortex are activated by retrieval processes for pronunciation or naming tasks. Interestingly, both the left STG and pIFG are excluded from these processes in these findings.

Although language processing is largely lateralized to the left hemisphere, the language system is organized bilaterally. Various tests are used to determine localization: Wada testing, which uses intracarotid sodium Amytal injections (Zatorre, 1989), is used to determine relative lateralization of language and memory functioning across hemispheres (Binder et al. 1996); dichotic listening tests are a noninvasive measure which uses auditory stimuli presentations to assess speech lateralization (Geffen & Caudrey, 1981). Many studies provide strong evidence for differences between the hemispheres in processing acoustic/ speech information (Hickok, 2012). One such area is prosody; variations in tone which illustrate emotion/ affect. (Glasser & Rilling, 2008). The posterior right MTG is responsible for representing meaningful patterns in prosodic speech, and fMRI has demonstrated that the area is connected bilaterally to the frontal lobe. Emotional prosodic sequences were then shown to activate the right IFG, whereas linguistic prosodic sequences selectively activated the left IFG (Ethofer et al. 2006). Furthermore, lesion studies have illustrated prosodic functioning of the right MTG and right STG, whilst subcortical lesions have also been shown to cause aprosodia (Darby, 1993). Damage to the right MTG pathway or its subcortical components hinder prosodic processing (Glasser & Rilling, 2008). Conversely, damage to the left STG alone most likely does not cause deficits in multimodal language comprehension. Lesions in the STG which involve adjacent MTG result in pure word deafness; a syndrome in which there is difficulty decoding complex signals in speech, but comprehension at a semantic level is preserved (Binder et al. 1997). Additionally, Hickok (2012) states that severe speech perception deficits can result from bilateral lesions in the superior temporal lobe, whilst electrical stimulation to the left ITG and MTG cause anomia, or transient sensory aphasia (Duffau et al. 2005; Boatman et al. 2000).

Aphasia is another acquired communication disorder caused by damage to the language system. There are many types of aphasia, all of which hinder an individual's ability to process language. Damage to the AF is known to cause conduction aphasia, in which auditory comprehension remains intact, speech production fluent, yet speech repetition is poor. DTI tractography and subcortical stimulation to this bundle causes phonological and syntactical errors (Chang et al. 2015). PET evidence also points to damage to the supramarginal gyrus as the cause of conduction aphasia (Habib and Demonet, 1996). Wernicke's aphasia is characterized by impaired speech comprehension, and fluent speech but frequent paraphasias or incorrect word selection. It is most commonly caused by damage to the left posterior temporo-parietal cortex (Robson et al. 2013). However, the nature of expressive and receptive disturbances in Wernicke's aphasia is still not understood, and some suggest it may not be the site of language comprehension itself (Habib & Demonet, 1996). Broca's aphasia is characterized by agrammatism, impaired fluency and disorder in articulation. Patients often has difficulty with comprehension if grammatical cues are central to the sentence's semantics. (Habib & Demonet, 1996). In typical Broca's aphasia, the lesion must extend beyond BA 44 and 45, towards the more interior prefrontal zones. Damasio and Tranel (1993) found BA 46/47 to be a mediation area for word retrieval, and this may explain the hallmark agrammatism.

REFERENCES

- Bates, E., & Dick, F. (2000). Beyond Phrenology: Brain Language in The Next Millennium. *Brain and Language*, 71, 18-21.
- Binder, J. R., Frost, J. A., Hammeke, T. A., Cox, R. W., Rao, S. M., & Prieto, T. (1997). Human brain language areas identified by functional magnetic resonance imaging. *Journal of Neuroscience*, 17, 353-362.
- Boatman, D., Gordon, B., Hart, J., Selnes, O., Miglioretti, D., & Lenz, F. (2000). Transcortical sensory aphasia: revisited and revised. *Brain*, 123(8), 1634-1642.
- Castillo, E. M., Simos, P. G., Davis, R. N., Breier, J., Fitzgerald, M.E., & Papanicolaou, A. C. (2001). Levels of word processing and incidental memory: dissociable mechanisms in the temporal lobe. *Neuroreport*, 12, 3561-3566.
- Catani, M., Jones, D. K., & Ffytche, D. H. (2005). Perisylvian language networks of the human brain. *Ann Neurol*, 57, 8-16.
- Chang, E. F., Ragy, K. P., & Berger, M. S. (2015). Contemporary model of language organization: an overview for neurosurgeons. *J Neurosurg*, 122(2), 250-61. DOI: 10.3171/2014.10.JNS132647.
- Crosson, B. (1985). Subcortical functions in language: a working model. *Brain and Language*, 25, 257-292.
- Damasio, A. R., & Tranel, D. (1993). Nouns and verbs are retrieved with differently distributed neural systems. *Proceedings of the National Academy of Sciences, USA*, 90, 4957-4960.
- Darby, D. G. (1993). Sensory Apraxia: A Clinical Clue to Lesions of The Inferior Division of The Right Middle Cerebral Artery? *Neurology*, 43, 567-572.
- Demonet, J. F., Thierry, G., & Cardebat, D. (2005). Renewal of the Neurophysiology of language: Functional neuroimaging. *Physiol Rev*, 85, 49-95. DOI:10.1152/physrev.00049.2003.
- Duffau, H., Gatignol, P., Mandonnet, E., Peruzzi, P., Tzourio-Mazoyer, N., & Capelle, L. (2005). New insights into the anatomofunctional connectivity of the semantic system: a study using cortico-subcortical electrostimulations. *Brain*, 128, 797-810.
- Ethofer, T., Anders, S., Erb, M., Herbert, C., Wiethoff, S., Kissler, J., Grodd, W., & Wildgruber, D. (2006). Cerebral Pathways in Processing of Affective Prosody: A Dynamic Causal Modelling Study. *Neuroimage*, 30, 580-587.
- Friederici, A. D. (2009). Pathways to Language: fiber tracts in the human brain. *Trends in Cognitive Science*, 13(4), 175-181. DOI: 10.1016/j.tics.2009.01.001
- Geffen, G., & Caudrey, D. (1981). Reliability and Validity of the Dichotic Monitoring Test for Language Laterality. *Neuropsychologica*, 19(3), 413-423.
- Glasser, M. F., & Rilling, J. K. (2008). DTI Tractography of the human brain's language pathways. *Cerebral Cortex*, 18, 2471-2482.
- Habib, M., & Demonet, J. F. (1996). Cognitive neuroanatomy of language: The contribution of functional neuroimaging. *Aphasiology*, 10(3), 217-234. DOI: 10.1080/02687039608248409
- Hickok, G. (2012). The cortical organization of speech processing: Feedback control and predictive coding the context of a dual-stream model. *Journal of Communication Disorders*, 45, 393-402.
- Hickok, G., & Poeppel, D. (2004). Dorsal and ventral streams: a framework for understanding aspects of the functional anatomy of language. *Cognition*, 92, 67-99.
- Howard, D., Patterson, K., Wise, R., Brown, W. D., Friston, L., Weiller, C., & Frackowiak, R. (1992). The cortical localization of the lexicons: PET evidence. *Brain*, 115, 1769-1782.
- Jonas, S. (1982). The thalamus and aphasia, including transcortical aphasia: a review. *Journal of Communication Disorders*, 15, 31-41.

- Lurito, J. T., & Dziedzic, M. (2001). Determination of cerebral hemisphere language dominance with functional magnetic resonance imaging. *Neuroimaging Clin. N. Am.*, 11, 355-363.
- Mesulam, M. M. (1990). Large scale neurocognitive networks and distributed processing for attention, language, and memory. *Annals of Neurology*, 28, 597-613.
- Narain, C., Scott, S. K., Wise, R. J., Rosen, S., Leff, A., Iversen, S. D., et al. (2003). Defining a left-lateralized response specific to intelligible speech using fMRI. *Cerebral Cortex*, 13, 1362-1368.
- Parker, G. J. M., Luzzi, S., Alexander, D. C., Wheeler-Kingshott, C. A. M., Ciccarelli, O., & Lambon Ralph, M. A. (2005). Lateralization of ventral and dorsal auditory-language pathways in the human brain. *NeuroImage* 24, 656–666. DOI:10.1016/j.neuroimage.2004.08.047
- Rizzolatti, G., & Arbib, M. A. (1998). Language within our grasp. *Trends in Neurosciences*, 21(5), 188-194.
- Robson, H., Zahn, R., Keidel, J. L., Binney, R. J., Sage, K., & Lambon Ralph, M. A. (2013). The anterior temporal lobes support residual comprehension in Wernicke's aphasia. *Brain*, 137(3), 931–943.
- Szwed, M., Dehaene, S., Kleinschmidt, A., Eger, E., Valabregue, R., Amadon, A., & Cohen, L. (2011). Specialization for written words over objects in the visual cortex. *Neuroimage*, 56(1), 330-344. DOI: 10.1016/j.neuroimage.2011.01.073.
- Zatorre, R. J., Evans, A. C., Meyer, E., & Gjedde, A. (1992). Lateralization of phonetic and pitch discrimination in speech processing. *Science*, 256, 846-849.