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Discuss the strengths and weaknesses of the classical model of language in the brain.

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Abstract

This essay evaluates the classical model by focusing on its assumption that one pathway, the arcuate fasciculus (AF), connects posterior and anterior regions. The abilities and impairments of patients with AF damage, structural imaging and functional imaging suggest that the AF is a useful but oversimplified account of the neural processing stream for mapping sound to articulations. Although recent evidence implicates the extreme capsule pathway in semantic processing, a revised AF can connect the same significant brain regions, demonstrating the classical model's explanatory power. The classical model fails to explain data implicating the uncinate fasciculus pathway in semantic processing.

Utilizing language deficits accompanying brain lesions, neurologists during the 19th and 20th centuries created the classical model, the first family of models of language in the brain (Tremblay & Dick, 2016). This essay will understand the term, “classical model,” by its recent version illustrated in Geschwind’s (1979) article, “Specializations of the human brain.” In this version, spoken language production and comprehension are subserved by one white matter pathway, the arcuate fasciculus (AF), connecting Wernicke’s area and Broca’s area in the left hemisphere. This essay focuses on the strengths and weaknesses of the classical model’s assumption that the AF is the one pathway for spoken language. Opposingly, present-day researchers hold that multiple pathways subserve spoken language in dorsal and ventral streams (Hickok & Poeppel, 2004, 2007; Dick & Tremblay, 2012). The dorsal stream, containing pathways located superiorly, maps sound to articulations subserving phonological processing while the ventral stream, containing pathways located more inferiorly, subserves semantic processing. By analyzing diffusion tensor imaging (DTI) studies, functional imaging studies, and neurological patients, this essay conveys that the classical model’s AF is a generally accurate but oversimplified account of the dorsal stream. Then, by evaluating DTI, functional imaging and transient lesion studies, this essay demonstrates that a revised version of the classical model’s AF can explain data implicating a ventrally located pathway, the extreme capsule, in semantic processing. However, this essay finds that the classical model fails to explain functional and structural imaging data supporting the role of the uncinate fasciculus pathway in semantics.

DTI studies, which track the flow of water molecules in the brain to illuminate anatomical white matter pathways, demonstrate the anatomical plausibility of the AF; however, these studies have decomposed the AF into multiple pathways suggesting that the classical model’s AF is oversimplified (Glasser & Rilling, 2008; Catani et al., 2005). This essay refers to Broca’s area as including the pars opercularis and pars triangularis while Wernicke's area refers to the posterior superior temporal gyrus (pSTG). According to Catani et al.'s (2005) DTI method, the AF is composed of one direct pathway linking the pSTG and middle temporal gyrus (MTG) with Broca's area, as well as an indirect pathway linking Wernicke's area with the inferior parietal cortex (IPC) and then the IPC with Broca's area. According to Glasser and Rilling's (2008) DTI method, the AF consists of two direct pathways: one that terminates in the pSTG and another that terminates in the MTG, while both terminate anteriorly in Broca's area. Although these DTI studies postulate different partitions, this essay will not evaluate which is best. Importantly, these studies both converge on the suggestion that the classical model's proposed AF anatomically exists but is oversimplified.

Evidence that damage restricted to the AF can cause conduction aphasia (CA) verifies the classical model's attribution of the AF to linking sound with speech output. Impaired repetition with intact comprehension is emphasized in CA; however, CA also includes phoneme errors in speech (Damasio & Damasio, 1980; Goodglass, 1992; Geschwind, 1965). In the classical model, CA occurs by the disconnection between Wernicke's area and Broca's area via damage to the AF (Geschwind, 1965). In support of the classical model, Jones et al. (2014) reported that patients with damage restricted to the AF were impaired at word and/or nonword auditory repetition. Further supporting the importance of the AF in linking sound to speech output, Duffau et al. (2009) gave patients transient lesions restricted to the white matter of the AF by direct intracranial brain stimulation during picture naming and counting tasks. Although Duffau et al. (2009) did not investigate repetition, transient lesions to the AF caused phoneme errors in counting and naming tasks. Duffau et al.'s (2009) and Jones et al.'s (2014) findings support that damage restricted to the AF can disrupt phonological processing and the mapping of sound to articulations. The aforementioned findings are consistent with the classical model's claims for the

AF and suggest that the dorsal stream is at least partially facilitated by the classical model's AF.

Functional imaging studies, together with the aforementioned data, demonstrate the functional significance and anatomical plausibility of the AF, supporting that the classical model's AF is important for mapping sound to speech output. Flinker et al. (2015) used electrocorticography (ECoG), which reads neural activity directly from the cortical surface at high resolution, to record brain activity during auditory word repetition. Wernicke's area activated immediately after participants received auditory stimuli, followed by activity in Broca's area and then the motor cortex (Flinker et al., 2015). The ECoG results demonstrate the plausibility that information propagates across the AF from Wernicke's to Broca's as the classical model suggests; however, Flinker et al. (2015) only collected from left hemisphere cortical areas.

Investigating the functional significance of the classical model's AF requires functional imaging of the entire brain to determine whether Wernicke's area and Broca's area are important compared to all brain areas. Saur et al. (2008) provide such a study using functional magnetic resonance imaging (fMRI), which measures time-varying neural activity at a lower temporal resolution than ECoG by detecting fluctuations in oxygen concentration (Glover, 2011; Jacques et al., 2016). Saur et al. (2008) investigate which brain regions are important for mapping sound to speech output by subtracting fMRI activations in auditory word repetition from activations in auditory nonword repetition, because nonwords are harder for linking sound to articulations. Out of the entire brain, Wernicke's area and Broca's area were among the few regions significantly more activated during nonword repetition, suggesting that Wernicke's area and Broca's area are particularly important. In conjunction with the aforementioned DTI and CA data, Saur et al.'s (2008) and Flinker et al.'s (2015) findings provide strong converging evidence that the classical model's AF is an important pathway in the contemporary notion of the dorsal stream.

In contrast to the aforementioned studies which support the classical model's AF, patients with AF damage but normal repetition suggest that the classical model oversimplifies the pathway for mapping sound to articulations. Selnes et al. (2002) report that a patient with severe AF damage, as seen by DTI, had normal repetition. Similarly, Shuren et al. (1995) report a patient with AF damage by surgical resection also with normal repetition. The variability in the relationship between AF damage and repetition deficits necessitate a revision of the classical model to explain these inconsistencies (Berthier et al., 2012). Glasser and Rilling (2008) and Catani et al. (2005) both partitioned the AF into multiple segments, so the aforementioned variability could be explained by postulating that only some of these segments are necessary for repetition. Unfortunately, the studies of Selnes et al. (2002), Shuren et al. (1995), and Jones et al. (2014) can not evaluate this hypothesis since they did not distinguish which parts of the AF had damage, therefore future studies are required that report which AF segments are damaged. Another explanation is that alternative pathways, other than the left hemisphere AF, also facilitate auditory repetition (Glasser & Rilling, 2008; Berthier et al., 2012). The classical model's account of the neural processing stream which maps sound to articulations must be revised either with an AF consisting of multiple segments with varying functional significance or with more than one pathway.

DTI, fMRI and transient lesion studies suggest the extreme capsule (EmC), a white matter pathway, is involved in semantic processing; however, the AF could instead subserve the functions ascribed to the EmC, demonstrating the classical model's explanatory power (Dick & Tremblay, 2012; Glasser & Rilling, 2008). In order to identify brain regions subserving semantic processing, Saur et al. (2008) subtracted brain activations occurring while participants listened to meaningless sentences from activations during meaningful sentence listening. Meaningful auditory comprehension relied on the MTG and pars orbitalis. Using a DTI method, Saur et al. (2008)

identified the EmC as most likely to connect the MTG and pars orbitalis, but a different pathway could still link these regions. DTI studies demonstrate that the AF terminates in the MTG and Broca's area, and a short frontal lobe pathway links Broca’s area with the pars orbitalis (Glasser & Rilling, 2008; Catani et al., 2005; Lemaire et al., 2013). Therefore, the AF and this frontal pathway could connect the functionally significant regions.

Duffau et al. (2005) found that intracranial stimulation directly applied to the EmC causes semantic speech errors in picture naming (Kier et al., 2004; Dick & Tremblay, 2012; Duffau et al., 2014). However, the stimulation sites are close to the AF pathway ending in the MTG, therefore AF damage can explain the semantic speech errors (Glasser & Rilling, 2008). The hypothesis that the AF terminating in the MTG instead subserves these semantic functions is consistent with Hickok and Poeppel’s (2007) proposal for the posterior MTG’s role as an interface between sound and meaning in the ventral stream. Saur et al.’s (2008) finding that the MTG is functionally significant for comprehension corroborates this view. Future studies involving more precise intracranial stimulation are needed. Although the classical model’s AF lacks MTG terminations, the classical model’s AF is useful in explaining the neuroanatomical correlates of both phonological and semantic processing pathways.

The classical model fails to account for data implicating another ventrally located white matter pathway, the uncinate fasciculus (UF), in semantic processing. DTI studies demonstrate the existence of the UF, which links the anterior left inferior frontal gyrus (LIFG) with Brodmann area (BA) 38 of the left anterior temporal lobe (ATL) (Devlin, 2009; de Schotten et al., 2012). If the left ATL and anterior LIFG are functionally significant for semantic processing, then both functional significance and anatomical plausibility support the UF’s role in semantic processing. Utilizing transcranial magnetic stimulation (TMS), a non-invasive method to induce transient lesions, Gough et al. (2005) found that TMS applied to the anterior LIFG impaired reaction time for deciding if two words are synonyms whereas TMS to the posterior LIFG caused no impairment (Walsh & Cowey, 2000). Although numerous functional imaging studies also support the anterior LIFG's importance in semantic processing, the demonstrated dissociation within the anterior and posterior LIFG is sufficient to implicate the anterior LIFG in semantic processing (Fiez, 1997).

Lesion studies and TMS studies converge on the left ATL's importance in semantic processing. Mummery et al. (2000) found that among six semantic dementia patients, BA 38 of the left ATL was consistently damaged and correlated significantly with the level of deterioration in semantic functions, suggesting the left ATL is important in semantic processing. However, these six patients also exhibited consistent damage to the MTG, an area implicated in semantic comprehension by Saur et al.'s (2008) fMRI findings, raising the possibility that damage to the MTG instead caused semantic deficits. Utilizing TMS, Holland and Lambon Ralph (2010) resolves this discrepancy by demonstrating that a precise transient lesion in the left ATL impaired participants' response time in generating the past tense of irregular verbs when given the present tense. Since participants can not rely on statistical regularities to form the past tense of irregular verbs, they rely on semantics to do so, demonstrating the importance of the left ATL in semantic processing (Holland & Lambon Ralph, 2010). Thereby, the UF is both anatomically plausible and functionally significant to subserve semantic processing, and the AF can not connect BA 38 with the anterior LIFG, suggesting that the classical model lacks a necessary ventral pathway.

This essay focuses on the strengths and weaknesses of the classical model's assumption that one pathway, the AF, can facilitate all spoken language functions. The classical model lays the foundations for the importance of the AF in phonological processing. DTI data and inconsistencies in the deficits of AF damaged patients demonstrate that the classical model has an oversimplified conception of the processing stream for mapping sound to articulations, now referred to as the dorsal stream. Furthermore, the AF can currently explain data implicating the EmC's importance in semantics, although future studies are needed to resolve the debate. However, evidence for the UF's importance in semantic processing can not be explained by the classical model, therefore the classical model must be revised to include the UF, one necessary pathway of the ventral stream. The classical model's assumption of one pathway is deficient; however, the classical model can still explain some key neuroanatomical correlates of spoken language processing streams.

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