# Functional heterogeneity within Broca's area

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Broca's area, traditionally defined as the triangular and opercular portions of the left inferior frontal gyrus (IFG), has been implicated in many linguistic processes, including phonological (Blumstein et al., 2005; Myers et al., 2009), lexical (Hagoort et al., 2004, 2009; Rodd et al., 2005; Schnur et al., 2009), and syntactic (Ben-Shachar et al., 2003, 2004; Friederici et al., 2006; Stromswold et al., 1996) processes. Furthermore, although originally argued to be specific to language (Broca, 1861), this region has now been implicated in a wide range of non-linguistic functions, including general working memory, cognitive control, arithmetic processing, goal-directed behavior, aspects of action representation, and music (e.g., Awh et al., 1996; Badre et al., 2005; Braver et al., 1997; Bunge et al., 2000; Cohen et al., 1994; Fadiga et al., 2009; January et al., 2009; Koechlin et al., 2003; Koelsch et al., 2002; Levitin & Menon, 2005; Novick et al., 2005; Piazza et al., 2006). Consequently, it has been a challenge to determine the function(s) of Broca's area, and no clear consensus has been reached.

However, it has also long been known that IFG is cytoarchitectonically heterogeneous, consisting of cortical patches with distinct cellular, myelination, and connectivity properties (Amunts et al., 1999, 2010; Brodmann, 1909; Petrides & Pandya, 1994). Given this structural heterogeneity, it may not be helpful to talk about "Broca's area" as a single region. In addition, the use of traditional group-based analyses may obscure functional differences among nearby but distinct sub-regions within Broca's area (Fedorenko et al., 2010).

We use individual-subject fMRI analyses across seven experiments (in each experiment participants performed a language task and one or more non-language tasks, each of which has been previously argued and/or shown to activate "Broca's area"). The results provide clear evidence for two functionally distinct sub-regions within Broca's area: an anterior portion (roughly corresponding to pars triangularis) and a posterior portion (roughly corresponding to pars opercularis). The anterior portion responds robustly to linguistic stimuli (sentences, presented visually or auditorily) but shows little or no response to non-linguistic tasks, including arithmetic, spatial and verbal working memory, three cognitive control tasks (Stroop and two versions of the multi-source interference task; Bush & Shin, 2006), and music. In contrast, the posterior portion responds robustly to demanding cognitive tasks (arithmetic, spatial and verbal working memory, and cognitive control tasks), but shows little response to linguistic stimuli, responding more strongly to pronounceable nonwords than sentences. This posterior portion of Broca's area has been argued by some (e.g., Duncan, 2001, 2010) to be a part of the larger network of regions that support goal-directed behavior, known as the "fronto-parietal", "task-related" or "multiple-demand" network.

Because the precise locations of the anterior and posterior functional sub-regions vary substantially across individuals (Amunts et al., 1999; Fedorenko et al., 2010; Tomaiuolo et al., 1999), traditional group analyses are unlikely to yield a clear picture of the functional organization of this region. Consequently, individual-subject functional-localization analyses that take into account differences in brain anatomy (e.g., Fedorenko et al., 2010; Hickok et al., 2009; Pinel et al., 2007) will be key for determining the computations conducted in different portions of Broca's area.

To conclude, referring to a particular activation as originating within "Broca's area" is ambiguous given the clear functional dissociation between anterior and posterior portions of this region. In order to understand how human cognition is implemented in the brain, we should stop using approximate anatomical locations as reference points and focus instead on providing careful functional characterization of key regions in each domain with the relevant brain regions defined consistently across studies and across labs.

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