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The contribution of the inferior parietal cortex to spoken language production

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ABSTRACT

This functional MRI study investigated the involvement of the left inferior parietal cortex (IPC) in spoken language production (Speech). Its role has been apparent in some studies but not others, and is not convincingly supported by clinical studies as they rarely include cases with lesions confined to the parietal lobe. We compared Speech with non-communicative repetitive tongue movements (Tongue). The data were analyzed with both univariate contrasts between conditions and probabilistic independent component analysis (ICA). The former indicated decreased activity of left IPC during Speech relative to Tongue. However, the ICA revealed a Speech component in which there was correlated activity between left IPC, frontal and temporal cortices known to be involved in language. Therefore, although net synaptic activity throughout the left IPC may not increase above baseline conditions during Speech, one or more local systems within this region are involved, evidenced by the correlated activity with other language regions.

1. Introduction

Indefrey and Levelt (2004) were the first to publish a meta-analysis of individual functional imaging experiments (over 80) on speech production. These studies had employed 'subtractive' contrasts between behavioral conditions using univariate statistical methods. Activated regions within the left frontal and temporal cortices, but not the inferior parietal cortex (IPC), were reported to be related to processing stages from lexical retrieval through to articulation (Levelt, 2001). One possibility for the apparent 'null' result in IPC was because the studies included in the meta-analysis had employed only single word tasks. This can be contrasted with a large lesion-deficit study, relating impaired aspects of speech production to lesion location identified on anatomical images (Borovsky, Saygin, Bates, & Dronkers, 2007). In this study, semantic information conveyed by utterances was reduced in those patients in whom infarction included, among other regions, the left inferior parietal lobe (specifically, the angular gyrus). This study had analyzed discourse level speech production. However, of the fifty patients studied, only one had infarction largely confined to the left parietal lobe. In all other cases with parietal involvement there was also infarction of the posterior temporal and/or frontal lobe; and presumably fairly extensive involvement of long white matter tracts, disconnecting remote left hemisphere cortical and subcortical regions (Catani & ffytche, 2005). Large lesions involving both gray and white matter are not ideal (but, in human pathology, all that are commonly available for research) when attempting to ascribe cognitive functions to particular cortical regions. In another lesion-deficit study, Fridriksson and colleagues (2010), suggested that hypo perfusion of the inferior supramarginal gyrus is associated with speech repetition deficits. Again in this study, lesions were not confined to the IPC.

Relatively small numbers of functional imaging studies have investigated discourse level spoken language production rather than single word or single sentence level production (Awad, Warren, Scott, Turkheimer, & Wise, 2007; Blank, Scott, Murphy, Warburton, & Wise, 2002; Braun, Guillemin, Hosey, & Varga, 2001; Brownsett & Wise, 2010; Haller, Radue, Erb, Grodd, & Kircher, 2005; Tremblay & Small, 2011). The majority of these studies used positron emission tomography (PET), in which movement-related and other artifacts are less evident than with conventional functional magnetic resonance imaging (fMRI), based on measuring the blood oxygen-level dependent (BOLD) signal (Gracco, Tremblay, & Pike, 2005). The PET studies related spoken language production networks with those involved in spoken language comprehension (Awad et al., 2007), and communication through sign language (Braun et al., 2001) and writing (Brownsett & Wise, 2010). Although none of the PET studies were designed to relate foci of activation to particular processing stages, they all reported a role for IPC, in particular the left angular gyrus, in the production of language, regardless of the output modality.

The motivation for these PET studies was to attempt to observe the entire networks engaged by everyday use of language. This is in

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contrast to the alternative approaches, which have attempted to attribute one or a few cortical regions to separate language processes such as phonological, semantic and syntactic levels of processing. Notwithstanding, the outcome of many of these latter studies has been to show a considerable degree of overlap across the left cerebral neocortex (Vigneau et al., 2006). A particular example is the left posterior middle temporal gyrus and the inferior frontal gyrus, important components of a semantic network according to Binder and colleagues (2009) but also central to the processing of syntax according to others (Papoutsi, Stamatakis, Griffiths, Marslen-Wilson, & Tyler, 2011); one conclusion from this is that attempting a 'neophrenology' of language can only be partially successful, and such a complex cognitive process can equally be represented as a distributed network without attempting detailed regional associations between function and anatomy.

The difficulties of separating signal from noise have discouraged the study of spoken language production with fMRI; although fMRI based on arterial spin labeling may offer an alternative to rival PET imaging of conversational speech production (Kemeny, Ye, Birn, & Braun, 2005). A number have used brief utterances of syllables and single words to investigate motor-sensory aspects of speech production (for example, Bohland & Guenther, 2006; Guenther, Ghosh, & Tourville, 2005; Riecker et al., 2005). In one MRI study investigating single sentence production (e.g. '*The child throws the ball*'), tasks were confined to epochs of 2 s (Haller et al., 2005). In that study, when compared to sentence reading, sentence production was associated with activations of left inferior and medial frontal gyri, right insula and the left superior parietal lobule. In another fMRI study that investigated propositional speech production, speech-related activity in the left angular gyrus is apparent in one of the figures, although this was small in spatial extent relative to extensive left inferolateral temporal and dorsolateral frontal activity (Dhanjal, Handunnetthi, Patel, & Wise, 2008). This latter study relied on image acquisition with sparse-sampling (Hall et al., 1999), in which functional imaging data were acquired during brief periods when the subject's spoken output was interrupted to minimize head movements and other sources of fMRI artifact related to speech production. The technique of sparse-sampling has been recently used to clarify the contribution of the pre-supplementary motor, ventral premotor, cingulate, and pars triangularis to motor response selection in speech production (Tremblay & Small, 2011).

A further issue in language studies relates to the nature of the baseline task. This can be of particular importance when assessing the role of IPC when data are analyzed with univariate statistical methods. Parts of the IPC form a component of the so-called default mode network. Activity in this network increases at 'rest' or when a task is not cognitively 'effortful', and it has proved to have a very reproducible distribution (Buckner, Andrews-Hanna, & Schacter, 2008; Esposito et al., 2006; Gusnard & Raichle, 2001; Raichle et al., 2001). It has been argued (Binder et al., 2009; McKiernan, D'Angelo, Kaufman, & Binder, 2006) that the default mode network is associated with the internal generation of spontaneous stimulus-independent thoughts, which will engage the semantic processes also involved in language processing. Therefore, 'subtractive' contrasts may mask important language-related regions, depending on the chosen baseline condition. This was the subject of the study by Seghier and colleagues (2010), in which careful use of contrasts between a number of conditions separated single word semantic processes from activity related to the default mode network in the left angular gyrus. It was also the motivation for including a cognitively 'effortful' numerical task as one of the baseline conditions in the language studies of Awad and colleagues (2007) and Brownsett and Wise (2010).

The objective of the present study was to investigate the participation of the IPC in spoken language production. The study employed a similar design and image acquisition methodology to those used by Dhanjal and colleagues (2008). However, in addition to univariate contrasts, group temporal concatenation independent component analysis (ICA) was used to investigate correlated activity over time across distributed brain regions (Beckmann & Smith, 2004). This approach has two advantages. It is able to separate signals within distributed functional brain networks from noise. This 'noise' may be created by head movement and physiological fluctuations, such as varying arterial carbon dioxide levels that may occur during the breathing control associated with speaking. Most importantly, ICA can reveal distinct but anatomically overlapping networks, corresponding to functionally different activation time courses intermixed within a single voxel (for example, see Leech, Braga. R., & D., 2012; Leech, Kamourieh, Beckmann, & Sharp, 2011). This distinction will not be apparent in a standard subtractive analysis. A further motivation for the present study arose from the publication by Smith and colleagues (2009). These authors demonstrated that correlated activity within separable distributed functional networks was present in 'resting state' fMRI data acquired from healthy subjects (Smith et al., 2009). When relating the anatomical distribution of these networks to a central database of regional 'activations' obtained from many functional imaging studies, a largely left-lateralized network distributed between inferior parietal, inferolateral temporal and posterior frontal cortices corresponded most closely with a cohort of functional imaging studies that had investigated some aspects of language processing. Our hypothesis was that this left-lateralized network (including the IPC) would be revealed by ICA to be engaged in the spoken language production condition (Speech) but not when the subjects performed a baseline task of non-communicative repetitive movements of the tongue (Tongue). In particular, we predicted that analysis with ICA would prove more sensitive than a conventional subtraction contrast between conditions, using univariate statistics, in demonstrating the contribution of IPC to the production of discourse level spoken language production.

2. Materials and methods

2.1. Participants and fMRI procedure

Twenty-three right-handed, native English speakers participated after giving informed written consent. The data from two participants were excluded because of excessive movement (>4 mm in any plane), one performed very poorly on the speech production task and a fourth showed unexpected brain pathology. Therefore, 19 subjects were included in the final analysis (13 females; mean age, 30 years; range, 22–62 years). Approval for the study was provided by the ethics committee for the North West Thames region.

MRI data were obtained on a Philips Intera 3.0 Tesla scanner using dual gradients, a phased array head coil, and sensitivity encoding (SENSE) with an undersampling factor of 2. A "sparse" fMRI design (Hall et al., 1999) was used to minimize movement- and respiratory-related artifact associated with speech (Gracco et al., 2005; Mehta, Grabowski, Razavi, Eaton, & Bolinger, 2006). Tasks were performed in response to specific visual stimuli during an epoch of 7 s (s). Following this, a fixation cross was displayed which was the cue for the subjects to discontinue the task. 0.75 s later whole brain functional imaging data was acquired over 2 s. The cycle was then repeated. This technique, to acquire data after task-related head movement and immediate speech-related respiration has temporarily ceased, is made possible due to the delayed onset of the hemodynamic response function (HRF) and its persistence for >10 s.

Functional MR images were obtained using a $T2^{*}$-weighted, gradient-echo, echoplanar imaging (EPI) sequence with whole-brain