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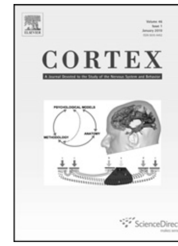

Research report

On the selection of words and oral motor responses: Evidence of a response-independent fronto-parietal network

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ABSTRACT

Several brain areas including the medial and lateral premotor areas, and the prefrontal cortex, are thought to be involved in response selection. It is unclear, however, what the specific contribution of each of these areas is. It is also unclear whether the response selection process operates independent of response modality or whether a number of specialized processes are recruited depending on the behaviour of interest. In the present study, the neural substrates for different response selection modes (volitional and stimulus-driven) were compared, using sparse-sampling functional magnetic resonance imaging, for two different response modalities: words and comparable oral motor gestures. Results demonstrate that response selection relies on a network of prefrontal, premotor and parietal areas, with the pre-supplementary motor area (pre-SMA) at the core of the process. Overall, this network is sensitive to the manner in which responses are selected, despite the absence of a medio-lateral axis, as was suggested by Goldberg (1985). In contrast, this network shows little sensitivity to the modality of the response, suggesting of a domain-general selection process. Theoretical implications of these results are discussed.

1. Introduction

Response selection occurs at the interface between cognitive and motor systems; it is a central component in planning actions. Despite the importance of this process, it is unclear whether different modes of response selection are implemented through similar or distinct neural networks. Selection can be implemented in many different ways, ranging from volitional to stimulus-driven. Volitional response selection corresponds to the most internally controlled selection mode, requiring the awareness of selecting or rejecting possible responses, and a decision of which response to produce from among several equally appropriate response alternatives (Jahanshahi and Frith, 1998). At the opposite end of the spectrum, stimulus-driven selection corresponds to the least internally controlled mode, whereby the context determines the response to be performed, leading to a "forced choice". While developed mainly to characterize simple motor actions, such as button presses, these concepts also apply to the production of more complex actions, such as spoken language

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(LNG) production. Volitional selection occurs, for instance, in verbal fluency and verb generation, tasks widely used as indexes of frontal lobe function (e.g., Frith et al., 1991; Milner, 1964). Forced selection occurs, for example, in picture naming and word repetition.

Currently, there is little attention focusing on incorporating response selection into contemporary models of LNG and speech. One important question is whether response selection is a domain-general process, or, alternatively, whether there are number of specialized selection processes across different domains and/or tasks. The existence of domain-general processes has important theoretical implications for modelling of spoken LNG behaviour. Contemporary models of LNG (e.g., Indefrey and Levelt, 2004) detail LNG-specific processes, such as lexical selection, morphophonological code retrieval and phonetic encoding, to the exclusion of generalized neural processes that might be shared across related behaviours. Similarly, speech production models (e.g., Guenther et al., 2006; Riecker et al., 2005) often either ignore higher-level motor aspects or rely on poorly defined and very general constructs such as motor planning/preparation as representing domain-general processes. Despite the lack of attention that domain-general processes have received in models of spoken LNG production, there is some evidence suggesting a link between LNG and other functional motor behaviours. For instance, behavioural studies have shown a connection between speech and hand gestures (Gentilucci et al., 2001; Gentilucci, 2003), and between LNG and oral motor gestures (Alcock et al., 2000; Alcock, 2006). Moreover, left hemisphere aphasic patients with speech-related impairments often have concomitant non-verbal oral movement impairments (Alcock et al., 2000; Alcock, 2006). The inclusion of non-verbal oral motor exercises in the treatment of acquired and developmental speech disorders is a common practice among speech–LNG pathologists (Skahan et al., 2007) despite the controversy that surrounds it (Ballard et al., 2003; Kimura and Watson, 1989; Ludlow et al., 2008; Weismer, 2006; Ziegler, 2003). One possibility is that the speech/LNG production system relies on processes that are used by other non-speech and LNG behaviours. A global understanding of brain functioning requires a thorough understanding of the extent to which neural systems supporting different behaviours overlap with one another. Examining the extent to which speech production and response selections reflect a domain-general processes was one of the objectives of the current study.

Another aspect of response selection that needs to be clarified concerns its neural implementation. Several brain areas, including the pre-supplementary motor area (pre-SMA), the anterior cingulated area (ACC), the dorso-lateral prefrontal cortex (DLPFC) and the inferior frontal gyrus (IFG), have been implicated in response selection. The pre-SMA has a connectivity pattern that is characterized by important projections from executive centers in the prefrontal cortex, in particular from the DLPFC (Lu et al., 1994; Luppino et al., 1993; Wang et al., 2005), suggesting an involvement in higher-order aspects of action. In line with this hypothesis, it has been shown recently, using functional magnetic resonance imaging (fMRI), that the presence of uncertainty regarding which motor response to prepare (random *vs* regular stimulus presentation) is associated with enhanced activity in the pre-SMA as well as the dorsal premotor area (PMAd), suggesting a role for these areas in response selection (Sakai et al., 2000). The pre-SMA, however, appears to be modulated by the manner in which responses are selected, being more strongly active for volitional than forced selection of overt (Alario et al., 2006; Etard et al., 2000; Tremblay and Gracco, 2006) and covert words (Crosson et al., 2001), as well as for the volitional selection of finger movements (e.g., Deiber et al., 1996; Lau et al., 2004, 2006; Oostende et al., 1997; Sakai et al., 2000; Ullsperger and von Cramon, 2001). A role for the pre-SMA in response selection, however, is not without controversy. It has been suggested that the pre-SMA is not involved in response selection but instead in response set reconfiguration or in resolving conflict among competing response alternatives (Garavan et al., 2003; Nachev et al., 2005; Rushworth et al., 2002, 2004;) or in response initiation (Mueller et al., 2007). Proponents of these alternative hypotheses have suggested that the PMA and the anterior cingulate area (ACC), but not the pre-SMA, are involved in response selection. Thus, although it is clear that frontal premotor areas play a role in response selection, the specific contribution of each area to this process remains ambiguous.

Aside from the premotor areas, different parts of the prefrontal cortex have also been implicated in response selection: the left IFG and the DLPFC. Several studies have shown that activity in the left IFG is modulated by response selection, being more strongly active for volitional word selection compared with constrained word selection (Abrahams et al., 2003; Crosson et al., 2001; Etard et al., 2000; Phelps et al., 1997; Thompson-Schill et al., 1997; Tremblay and Gracco, 2006). This finding suggests that the left IFG is involved in the selection of words. Alternatively, the IFG might be involved in the selection of all kinds of motor responses, not restricted to the production of words (Thompson-Schill et al., 1997). This latter interpretation, however, is challenged by the fact that selection of motor responses (e.g., button presses), as well as spatial location, both appear to recruit the dorso-lateral prefrontal area (DLPFC) (Frith et al., 1991; Hyder et al., 1997; Jahanshahi et al., 1999a, 1999b; Lau et al., 2004; Rowe et al., 2000; Schumacher and D'Esposito, 2002; Schumacher et al., 2007), but not the IFG, suggesting that the left IFG might be involved *only* in selecting words, not other types of responses. Recent repetitive transcranial magnetic stimulation (rTMS) experiments have shown that stimulation over the left DLPFC affects the manner in which responses (numbers and letters) are selected (Jahanshahi and Dirnberger, 1998). Word generation typically requires some linguistic processing to take place (e.g., semantic search), processes that are not involved in the selection of oral motor responses, such as finger movements, which might explain the absence of the IFG in many studies of finger movement selection, and its presence in the overwhelming majority of studies involving the production of words. In sum, although several brain areas (pre-SMA, ACC, PMA, DLPFC and IFG) appear to play a role in response selection, their precise contribution remains unclear. The goal of the present study was therefore to examine, using sparse-sampling fMRI (Eden et al., 1999; Edmister et al., 1999; Gracco et al., 2005), the contribution of these areas to volitional and forced response