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Research Report

The role of the basal ganglia and cerebellum in language processing

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ABSTRACT

The roles of the cerebellum and basal ganglia have typically been confined in the literature to motor planning and control. However, mounting evidence suggests that these structures are involved in more cognitive domains such as language processing. In the current study, we looked at effective connectivity (the influence that one brain region has on another) of the cerebellum and basal ganglia with regions thought to be involved in phonological processing, i.e. left inferior frontal gyrus and left lateral temporal cortex. We analyzed functional magnetic resonance imaging data (fMRI) obtained during a rhyming judgment task in adults using dynamic causal modeling (DCM). The results showed that the cerebellum has reciprocal connections with both left inferior frontal gyrus and left lateral temporal cortex, whereas the putamen has unidirectional connections into these two brain regions. Furthermore, the connections between cerebellum and these phonological processing areas were stronger than the connections between putamen and these areas. This pattern of results suggests that the putamen and cerebellum may have distinct roles in language processing. Based on research in the motor planning and control literature, we argue that the putamen engages in cortical initiation while the cerebellum amplifies and refines this signal to facilitate correct decision making.

1. Introduction

Houk proposed that the basal ganglia is involved in the embodiment (i.e. selection and/or initiation) of cortical patterns of activation for both planned behaviors and for thoughts (Houk, 2005). In contrast, he proposed that the cerebellum engages in online amplification and refinement of behaviors or thoughts as they are occurring, which provides an error correction mechanism for performance of the task. Cerebellar regulation of motor planning and control is well documented, particularly for reaching and acquiring targets (Thach, 1998). A coherent limb movement can be broken down into smaller component sub-movements, which include online error corrections (Barto et al., 1999; Fishbach et al., 2006; Ghez and Martin, 1982). Houk (2005) also proposed that the cerebellar role in refinement and amplification and the striatal role of embodiment could be involved in language processing. The current study is the first to look at effective

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connectivity of the cerebellum and basal ganglia during a language processing task. Both of these structures have connections with frontal regions and temporo-parietal regions thought to be involved in language processing in humans (Alexander et al., 1986; Clower et al., 2005; Dum and Strick, 2003; Middleton and Strick, 1994, 1996). In particular, the inferior frontal gyrus and lateral temporal cortex have been implicated in phonological processing (Bitan et al., 2005; Booth et al., 2002a).

It is being increasingly recognized that the cerebellum is involved in many cognitive processes including language processing (Desmond and Fiez, 1998). Studies using rhyming tasks to visually presented words have shown activation in bilateral cerebellum (Fulbright et al., 1999). Although some studies show that superior portion of the cerebellum is interconnected with lateral temporal cortex (Brodal, 1978; Schmahmann and Pandya, 1991; Vaudano et al., 1991), studies in primates show that the superior portion of the cerebellar hemisphere is predominantly interconnected with inferior frontal cortex, whereas the inferior portion is predominantly interconnected with parietal cortex (Brodal, 1978; Schmahmann and Pandya, 1997). Based on the role of the inferior frontal cortex in articulation and the parietal cortex in phonological short-term memory, Desmond and colleagues proposed that superior portion of right cerebellum (VI/Crus I) is involved in articulatory control, whereas the inferior portion (VII) of right cerebellum is involved in phonological working memory (Desmond et al., 1997). This was supported by their finding that superior cerebellum showed activation in articulation, rehearsal and verbal working memory, whereas inferior cerebellum only showed activation in verbal working memory (Chen and Desmond, 2005a; Desmond et al., 1997). In a subsequent event-related study that allowed an examination of the time course of activation, they showed that both encoding and maintenance was associated with activation in superior cerebellum (VI/Crus I), but that only maintenance was associated with activation in inferior cerebellum (VII/VIII) (Chen and Desmond, 2005b). They interpreted the superior activation as due to the need to rapidly translate the consonant string into an articulatory trajectory.

Several studies have shown that the basal ganglia is involved in various reading and language tasks. Greater accuracy of the detection of phonological anomalies is correlated with greater activation in left caudate nucleus and faster phonological processing is correlated with greater activation in left putamen (Tettamanti et al., 2005b). Detecting syntactical anomalies has also been associated with greater activation in left caudate nucleus (Moro et al., 2001). Abdullaev and Melnichuk (1997) placed depth electrodes in the head of the caudate nucleus in Parkinson's patients to measure population neuronal firing rates when these patients were performing a variety of cognitive tasks (Abdullaev and Melnichuk, 1997). They showed increased firing within 400–600 ms after stimulus onset during semantic processing by comparing lexical decision to words versus pseudo-words and increased firing within 1000–1200 ms after stimulus onset during phonological processing by comparing lexical decision to pseudo-words to non-words. They also showed that early neuronal firing in semantic processing was replicated in a categorization task (concrete versus abstract judgment) and that this activation was not associated with motor output. This study provides provocative evidence that the basal ganglia is involved in language processing. Comparing this study to an earlier report from the same group suggests that activation in the caudate nucleus seems to lag behind activation in left inferior frontal gyrus (Bechtereva et al., 1991). In his procedural/declarative model of language learning, Ullman (2001) proposes that the basal ganglia is part of a procedural system that is involved in the assembly of phonemes into words (Ullman, 2001).

Functional neuroimaging studies aim to identify network components that are selectively engaged by cognitive tasks. However, a network could shift from one behavioral goal to another not because of differences in the distribution of activations, but because of differences in the interactions among its components (Damasio, 1989; McIntosh, 2000; Mesulam, 1981, 1998). Analyses of effective connectivity (the modulatory influence that one brain region exerts upon another), and its non-directional counterpart known as functional connectivity (based on correlation of brain activation between regions), have, in fact, shown that network components can display task-dependent alterations in their interactions (Chaminade and Fonlupt, 2003; Homae et al., 2003; Horwitz et al., 1998; McIntosh et al., 1994; Pugh et al., 2000). Components of distributed networks serve multiple roles including the integration of convergent inputs, the binding of distributed information, the relay of information from one region to another, and the control of neural activity within other network components (Mesulam, 1998). Some studies have examined effective connectivity of the basal ganglia and cerebellum with cortical regions, but none have examined language processing. The cerebellum has been shown to influence parietal cortex during visual/motor imagery (Solodkin et al., 2004) and prefrontal cortex during recognition tasks (Nyberg et al., 1996). The basal ganglia has been shown to influence prefrontal regions during classification learning (Poldrack and Rodriguez, 2004) and object location learning (Honey et al., 2003).

In a previous study with adults, we used dynamic causal modeling to show that the cognitive demands of the reading task affect patterns of effective connectivity (Bitan et al., 2005). A spelling task was marked by converging influence from other brain regions on the intraparietal sulcus, whereas a rhyming task was marked by converging influence on the lateral temporal cortex, suggesting that these regions are sites of integration for processing task-selective information. In both tasks, modulating influences also converge on inferior frontal gyrus. We proposed that inferior frontal gyrus is involved in top-down modulation of task-selective regions in a way that differentially enhances their sensitivity to task relevant information. The goal of the current study was to examine the role of the basal ganglia and cerebellum in modulating cortical regions thought to be involved in phonological processing, i.e. left inferior frontal cortex and left lateral temporal cortex. Adults made rhyming judgments to words while undergoing functional magnetic resonance imaging (fMRI). In this task, three visual words were presented one after the other (e.g. hold–milk–cold, door–hope–soap, house–press–list) and the participant had to press a button indicating whether the final word rhymed with either of the