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The interaction of process and domain in prefrontal cortex during inductive reasoning

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ABSTRACT

Inductive reasoning is an everyday process that allows us to make sense of the world by creating rules from a series of instances. Consistent with accounts of process-based fractionations of the prefrontal cortex (PFC) along the left–right axis, inductive reasoning has been reliably localized to left PFC. However, these results may be confounded by the task domain, which is typically verbal. Indeed, some studies show that right PFC activation is seen with spatial tasks. This study used fMRI to examine the effects of process and domain on the brain regions recruited during a novel pattern discovery task. Twenty healthy young adult participants were asked to discover the rule underlying the presentation of a series of letters in varied spatial locations. The rules were either verbal (pertaining to a single semantic category) or spatial (geometric figures). Bilateral ventrolateral PFC activations were seen for the spatial domain, while the verbal domain showed only left ventrolateral PFC. A conjunction analysis revealed that the two domains recruited a common region of left ventrolateral PFC. The data support a central role of left PFC in inductive reasoning. Importantly, they also suggest that both process and domain shape the localization of reasoning in the brain.

1. Introduction

The prefrontal cortex (PFC) is a complex and diverse region of the brain that is critical in many higher level functions. In particular, executive functions have been broadly localized to the prefrontal cortex (e.g., Baddeley, 1986; Luria, 1966; Norman and Shallice, 1986). However, recently, various views aiming to better specify the location of individual processes have identified functional fractionations along the three directional axes. A gradient of representation has been posited along the rostro-caudal axis, with simple stimulus–response associations localized to more posterior areas and entire task-sets represented anteriorly (Badre and D'Esposito, 2009; Kim et al., 2011; Koechlin and Summerfield, 2007). Along the ventral–dorsal axis, the working memory processes of storage and manipulation have been localized to ventrolateral and dorsolateral PFC, respectively (Petrides, 2005; Rowe et al., 2000). Perhaps the first distinctions suggested were domain-based along the left–right axis. These models basically hold that the left hemisphere is the locus of verbal processing, while the right hemisphere is the seat of spatial processing (Kelley et al., 1998; Wagner et al., 1998). Evidence in support of this domain-based lateralization has come from loss of function in patients with lesions (e.g., McCarthy and Warrington, 1990; Ratcliff, 1979; Warrington and Rabin, 1970) as well as from healthy individuals (e.g., Smith et al., 1996). More recently and specific to the prefrontal cortex, the ROBBIA (Rotman-Baycrest Battery to Investigate Attention) model of executive functions suggests that distinctions along the left–right axis exist based on the process used (Stuss and Alexander, 2005). This model posits that criterion-setting processes, which allow the set up and selection of relevant task rules and are broadly defined as strategy production (Cabeza et al., 2003; Fletcher et al., 2000; Shallice, 2004), are localized to left lateral PFC, while monitoring and energization processes are found in right lateral and medial PFC, respectively (see Stuss, 2011; Vallesi, 2012, for recent reviews). How this process-based fractionation along the left–right axis of the prefrontal cortex is influenced by domain-based distinctions remains under-examined. In this study we consider the effects of domain on one criterion-setting process, inductive reasoning.

Inductive reasoning is the process of discovering a rule or pattern based on instances belonging to that rule. This complex process involves collecting and remembering instances of the rule, generating a hypothesis based on these instances, integrating new

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instances, and confirming the hypothesis through further observation (Crescentini et al., 2011). Supporting the ROBBIA model, left prefrontal cortex has consistently been shown to be a critical node for inductive reasoning. This has been seen in studies focused on split-brain patients (Gazzaniga and Smylie, 1984), patients with lesions (Reverberi et al., 2005a, 2005b) and healthy individuals (Crescentini et al., 2011; Goel and Dolan, 2000, 2004; Goel et al., 1997; Jia et al., 2011; Specht et al., 2009; Yang et al., 2009). Typically, though, inductive reasoning studies use verbal material. Thus these studies are less informative when addressing the effect of domain on localizations of inductive reasoning since both domain-based and process-based distinctions predict left lateralization in those cases. Rather, it is the spatial/non-verbal domain where conflicting predictions exist. Of inductive reasoning studies using non-verbal material, five have found activations in right PFC (always in conjunction with left PFC). Interestingly, none of these studies explained their results in terms of domain-based distinctions. Here we review these studies and the explanations given for the curious right PFC activations.

Specht and colleagues asked participants to complete a variant of the Wisconsin Card Sorting Test (WCST) in which the stimuli were non-verbalizable (Specht et al., 2009). Bilateral activations in dorsolateral and ventrolateral PFC were evidenced in the condition in which participants were required to induce the sorting rule when compared to either a rest condition or a condition in which the sorting rule was given. The rule given condition (when compared to rest), however, showed right-lateralized dorsolateral prefrontal cortex (DLPFC) activations and less extensive bilateral ventrolateral PFC activations. From these data the authors concluded that left DLPFC is particularly involved in inductive reasoning and hypothesis generation, while right DLPFC carries out selection and implementation of previously learned rules.

In Goel and Dolan (2000) participants had to classify drawings of novel animals based either on a given rule or through induction of a rule. A task by difficulty interaction showed an effect in right inferior PFC due to increased activation in the difficult rule induction condition and decreased activation in the rule application conditions. The authors concluded that the difficult rules required more evaluation of hypotheses than the easy rules and therefore attributed the right inferior PFC activation to hypothesis selection rather than hypothesis generation. Additionally, while both rule application and rule induction (compared to a perceptual baseline) showed bilateral PFC activations, the rule induction activations were strongly right-lateralized. The authors explained this right hemisphere dominance, in contrast to left-lateralized activations in deductive reasoning studies, by suggesting that the right hemisphere may have a special role in inference tasks, which are open-ended and often have no right or wrong answer, compatible with a role for this region in monitoring (see above). Bilateral activations in prefrontal cortex and increased activations in right-lateralized regions with increasing rule complexity were also seen in another study which examined non-verbal reasoning through a pattern finding task (Hampshire et al., 2011). Those authors did not discuss the specific role played by right PFC.

An fMRI study by Crescentini and colleagues also found bilateral PFC activations in a non-verbal reasoning task (Crescentini et al., 2011). In that study participants completed a Brixton task in which they needed to find and apply a spatial pattern to describe the movement of a colored circle among twelve positions. Comparisons of rule acquisition with rule following in this study showed bilateral mid-dorsolateral PFC activations. A closer examination of these data, however, revealed that the left and right frontal regions were differentially affected by task factors and therefore may underlie different processes. Activity in left DLPFC was modulated by rule difficulty with more activation for difficult compared to easy rules. In contrast, this area was unaffected when response time was included as a covariate, an analysis which right DLPFC did not survive. The authors did not further speculate on the specific processes performed by left and right DLPFC; however, a rule difficulty effect in left, rather than right, PFC is in discord with the results and account of the abovementioned studies.

Finally, Yang and associates asked older participants to perform a numerical inductive reasoning task (Yang et al., 2009). These authors found bilateral DLPFC activations and explained the bilaterality as a possible effect of aging.

The interpretations suggested by the authors of these studies may adequately explain the data found in their own study, however extending them to data from other studies is problematic. Yang and colleagues' role for aging cannot explain the data from the other four studies, all of which were conducted using younger adults. In contrast, a hypothesis selection account could explain the data from the five discussed studies; however it would suggest that all studies of inductive reasoning should show activity in right PFC, a fact that is challenged by the collection of studies that found only left-lateralized activity. However, a domain-based account which suggests that the domain of the task impacts the hemisphere(s) used during inductive reasoning can explain the results of all five studies as well as the absence of right PFC activation in verbal inductive reasoning studies. The critical test for this explanation is to examine verbal and non-verbal tasks using the same inductive reasoning paradigm with the same type of stimuli and a common set of participants. To the authors' knowledge, no such study has been completed.

The present study addresses whether the domain of the to-be-induced pattern affects the hemisphere(s) used during inductive reasoning. We completed an fMRI study using a novel pattern finding task which crucially included both spatial and verbal patterns composed of the same elements. The patterns were created from letters presented in varied spatial locations that formed either shapes/designs constituting a category (with random letters) or words belonging to a semantic category (with random locations). Participants were asked to infer the category (in the experimental condition) or apply a known rule which required working memory (in the control condition). The common stimuli allow us to make strong observations on the effects of domain on the lateralization of the inductive reasoning process. A prediction based solely on the process-based distinction would suggest that left-lateralized PFC activations will be present for both the verbal and spatial domains. A purely domain-based lateralization account would predict left-lateralized activations for the verbal domain and right-lateralized activations for the spatial domain. However, given the studies presented above, combined activations could also be expected, that is, left PFC activations for the verbal domain and bilateral activations for the spatial domain.

2. Material and methods

2.1. Participants

Twenty-one healthy university students (16 females; mean age=22.8, SD=.6, range 22–24) participated in the study. All were right-handed native Italian speakers with no known neurological or psychiatric problems. Additionally, all participants reported having normal color vision, which was confirmed with the Ishihara Color Vision Test (Ishihara, 1972). The study was approved by the ethical committee of "Istituto IRCCS E. Medea – La Nostra Famiglia." All participants gave written informed consent and were compensated for their time. Participants were naïve with respect to the specific aims and comparisons of the study. One female participant was subsequently excluded from all analyses due to a low rate of pattern discovery and difficulties synchronizing her performance and neuroimaging data.