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A gateway system in rostral PFC? Evidence from biasing attention to perceptual information and internal representations

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ABSTRACT

Some situations require us to be highly sensitive to information in the environment, whereas in other situations, our attention is mainly focused on internally represented information. It has been hypothesized that a control system located in the rostral prefrontal cortex (PFC) acts as gateway between these two forms of attention. Here, we examined the neural underpinnings of this 'gateway system' using fMRI and functional connectivity analysis. We designed different tasks, in which the demands for attending to external or internal information were manipulated, and tested 1) whether there is a functional specialization within the rostral PFC along a medial–lateral dimension, and 2) whether these subregions can influence attentional weighting processes by specifically interacting with other parts of the brain. Our results show that lateral aspects of the rostral PFC are preferentially activated when attention is directed to internal representations, whereas anterior medial aspects are activated when attention is directed to sensory events. Furthermore, the rostrolateral subregion was preferentially connected to regions in the prefrontal and parietal cortex during internal attending, whereas the rostromedial subregion was connected to the basal ganglia, thalamus, and sensory association cortices during external attending. Finally, both subregions interacted with another important prefrontal region involved in cognitive control, the inferior frontal junction, in a task-specific manner, depending on the current attentional demands. These findings suggest that the rostrolateral and rostromedial part of the anterior PFC have dissociable roles in attentional control, and that they might, as part of larger networks, be involved in dynamically adjusting the contribution of internal and external information to current cognition.

Introduction

A key aspect of higher cognition is the ability to voluntarily direct attention to the information that is currently most relevant. This information can either be something present in the sensory environment (i.e. external information) or something that exists without a direct correlate in the environment (i.e. internal information). In different situations, the relevance of these two types of information differs, requiring a control system that flexibly biases the allocation of attentional resources to external or internal information, depending on the current goals. In order to enable adaptive behavior, this system should further allow individuals to rapidly switch between the different sources of information and to integrate the information coming from these sources. These operations have recently been suggested to be carried out by a control system located in the rostral prefrontal cortex (PFC), the 'supervisory attentional gateway system' (Burgess et al., 2007a,b). According to this theory, the system plays a key role in the attentional selection between 'stimulus-oriented (SO) cognition' (i.e. attention toward stimuli external to the body) and 'stimulus-independent (SI) cognition' (i.e. attention toward internally represented information) and thus operates as a 'gateway' between the internal mental life and the mental life that is associated with interaction with the outside world.

This model is noteworthy since the rostral PFC is one of the brain regions currently most discussed and least understood. There are a large number of different findings and competing theoretical accounts of its functions. Some models suggest that the region is involved in the "coordination of information processing and information transfer between multiple cognitive operations" (Ramnani and Owen 2004, p. 193), others in the "processing of internally generated information" (Christoff and Gabrieli 2000, p.169), and again others in processes like "branching", "updating", or "planning" (Koechlin et al., 1999; Collette et al., 2007; Soon et al., 2008), to name but a few. During the last 10 years, an almost equal number of neuroimaging studies have been published supporting the one or the other account, meaning that the function of the rostral PFC remains a matter of current debate.

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The situation is aggravated by confusion in the nomenclature regarding this most frontal region of the brain. Some authors speak of the 'rostral PFC', others of the 'anterior frontal cortex', the 'frontopolar cortex', 'rostrolateral PFC', or just 'Brodmann area 10'.[1] Furthermore, the fact that structurally and functionally different subregions might exist within the rostral PFC is often not taken into account. The existence of such subregions, however, is suggested by a number of studies on the microarchitectonic, structural, and functional level. Ongur and colleagues (2003), for instance, identified three dissociable regions within the rostral PFC with different cytoarchitectonic properties, and a recent meta-analysis of 104 imaging studies provided further evidence of a functional specialization of at least two distinct subregions within the rostral PFC (Gilbert et al., 2006c). In the light of these findings, the conflicting results and competing models of rostral PFC function may not be mutually exclusive but may rather describe the function of different anatomical regions within rostral PFC.

However, to date, few imaging studies have been conducted that explicitly examine the question whether there is a functional dissociation of subregions within the rostral PFC. These studies provided first experimental evidence of a functional specialization of the rostral PFC along a medial–lateral dimension, with rostrolateral aspects being specifically involved in orienting attention to internal representations and anterior medial aspects in directing attention to information that is present in the sensory environment (Gilbert et al., 2005, 2006a,b). Based on these findings, Burgess et al. (2007a) formulated the 'gateway hypothesis of rostral PFC function', according to which a 'supervisory system' is located in the rostral PFC, which exerts control over the coordination of stimulus-independent and stimulus-oriented cognition. Within this system, the anterior rostromedial PFC is supposed to be involved in generating an attentional bias towards incoming perceptual information and the rostrolateral PFC in maintaining attention to internal representations.

Importantly, however, according to the model, both rostral PFC subregions are not sites of information processing per se but accomplish their function by "altering the flow of information between other parts of the cognitive system" (Burgess et al., 2007a, p. 292). Thus, the system is supposed to act as a routing system that modulates the flow of information. This description is reminiscent of the ideas of 'gating models', which assume that frontal regions interact with other cortical and subcortical regions in order to bias information processing. In particular, it has been suggested that interactions of the frontal cortex with the basal ganglia and the thalamus are the basis for controlling the access of incoming information to higher processing areas (Frank et al., 2001; Hazy et al., 2007; LaBerge 2002). In addition, accumulating evidence suggests that the PFC can modulate information processing in sensory association cortices depending on the current attentional demands (Hopfinger et al., 2000; Kastner et al., 1999; Giesbrecht et al., 2006).

Similar interactions can also be assumed to be essential for the proposed functions of the gateway system, especially as the SO-system is supposed to be able to afford an "amplification of input" and the SI-system to "ensure that the activation of representations is less determined by sensory input" (Burgess et al., 2007a, p. 292). However, the gateway hypothesis remains relatively vague on this point and, in particular, the neurofunctional interactions which may underlie the described attentional weighting processes are not specified. In the current study, we addressed this issue using functional magnetic resonance imaging (fMRI) and functional connectivity analysis. In the first step, we sought to investigate whether we could find additional support for the notion of a functional subdivision of the rostral PFC into a rostrolateral and an anterior medial part, and if so, in the second step, we aimed to assess whether these subregions bias attentional orienting towards external or internal information by specifically interacting with other parts of the brain.

In addressing these issues, we designed an experimental paradigm that imposes different demands on external or internal attending. Taking into account that most natural situations do not involve the processing of either solely internal or solely sensory information, we decided to vary the relative degree to which attention had to be directed to the different sources of information. Using these tasks, we hypothesized that if the gateway hypothesis is correct, 1) the degree to which attention is directed to external or internal information should be reflected in the differential activation pattern of a rostromedial and rostrolateral PFC subregion, and 2) these subregions should functionally interact with other brain regions in order to prioritize the processing of internal or external information depending on the current attentional demands.

Materials and methods

Subjects

Participants were 27 right-handed native speakers of German (14 females, 13 males; mean age: 24.56 ± 2.53 years). All participants were recruited from an academic environment and had normal or corrected to normal vision. Ethical approval from the local ethics committee and written informed consent were obtained prior to the experiments. Subjects were paid for their participation.

Experimental design

The experiment comprised three experimental tasks imposing different demands on attending to externally presented or internally represented information, respectively. In designing these tasks, we considered the prerequisites named by the authors of the gateway hypothesis for tasks stressing external or internal attending. According to Burgess et al. (2007b), an external attention task requires 1) that the information to be processed is currently available (i.e. present in the sensory environment), 2) that the attention is directed to external stimuli or stimulus features, and 3) that the operations involved prior to responding are relatively automatic or well-learnt. In contrast, a task stressing internal attending requires 1) that the information attended to is not currently being presented (i.e. not available in the sensory environment), 2) that this information is self-generated or comes from a previously witnessed episode, and 3) that the responses to be made are triggered by these internal representations.

In accordance with these characteristics, we designed three tasks engaging internal and external attending to a different degree. Importantly, we decided to vary the relative degree to which attention is directed to either type of information, instead of using the most extreme task variants (e.g. an internal task with no external stimulation at all). This was done for two reasons. Firstly, most natural situations do not exclusively involve the processing of either internal or external information but involve both types of information, just differing in the relative degree to which attention is directed to each of them. Secondly, we wanted to ensure greatest possible comparability between the internal and external tasks in all aspects, with the exception of the directing of attention to sensory or internally represented information. This requires the tasks to be closely matched with respect to the visual stimulation and the responses to be made (which is hardly accomplishable when comparing a task involving a reaction to sensory stimuli with a task that is performed entirely "in the head" of the participants).

All tasks had the same stimulation design and timing and were performed in short blocks. At the beginning of each block, subjects

[1] We will use the term "rostral PFC," as well as "rostrolateral" and "rostromedial" PFC. With respect to the literature, "rostrolateral PFC" is used for the part of rostral PFC with an x-coordinate >20 (see Christoff and Gabrieli 2000; Smith et al., 2007; Gilbert et al., 2006c) and "rostromedial PFC" for the part with an x-coordinate <20.