



Neural substrates of cognitive switching and inhibition in a face processing task



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ABSTRACT

We frequently need to change our current occupation, an operation requiring additional effortful cognitive demands. Switching from one task to another may involve two distinct processes: inhibition of the previously relevant task-set, and initiation of a new one. Here we tested whether these two processes are underpinned by separate neural substrates, and whether they differ depending on the nature of the task and the emotional content of stimuli. We used functional magnetic resonance imaging in healthy human volunteers who categorize emotional faces according to three different judgment rules (color, gender, or emotional expression). Our paradigm allowed us to separate neural activity associated with inhibition and switching based on the sequence of the tasks required on successive trials. We found that the bilateral medial superior parietal lobule and left intraparietal sulcus showed consistent activation during switching regardless of the task. On the other hand, no common region was activated (or suppressed) as a consequence of inhibition across all tasks. Rather, task-specific effects were observed in brain regions that were more activated when switching to a particular task but less activated after inhibition of the same task. In addition, compared to other conditions, the emotional task elicited a similar switching cost but lower inhibition cost, accompanied by selective decrease in the anterior cingulate cortex when returning to this task shortly after inhibiting it. These results demonstrate that switching relies on domain-general processes mediated by postero-medial parietal areas, engaged across all tasks, but also provide novel evidence that task inhibition produces domain-specific decreases as a function of particular task demands, with only the latter inhibition component being modulated by emotional information.

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Introduction

The ability to switch from one task to another is a common cognitive process in everyday life, which is also extensively studied in behavioral research (for a review, see Meiran, 2010; Monsell, 2003). It is well established that such switching induces some behavioral cost (e.g. increased reaction time [RT] and error rate), imputed to changes in executive control operations (e.g. Allport and Wylie, 2000). Changing the current cognitive state requires the disengagement from previous activity and the generation of a new task-set, which as a whole is called “task-set reconfiguration” (Monsell, 2003). Switching costs

may result from both of these reconfiguration processes and the carry-over of persisting task-set interference (Kiesel et al., 2010). Several paradigms of task-switching have been designed to differentiate between the inhibition of a first mental set (task) and the reconfiguration necessary to implement a new set (second task) (Arbuthnott, 2008; Hubner et al., 2003; Koch et al., 2004; see, e.g. Mayr and Keele, 2000; Mayr, 2002). This work suggests that, in addition to a simple interruption of the ongoing mental set, some backward inhibition of the preceding task is also necessary during this process, which may act to reduce competition from the previous task demands on the new one. However this process of inhibition is still debated (Kiesel et al., 2010) and its neural substrate remains unresolved.

Evidence for backward inhibition in task-switching is usually obtained by testing sequences of three alternating tasks in ABA order or in CBA order (for review, see Koch et al., 2010). Indeed, in ABA sequence, switching from A to B requires first to inhibit the ongoing mental processes engaged in A, so that returning to A shortly

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afterwards will be less efficient and requires stronger effort. This effect of returning to a previously inhibited task has therefore a measurable behavioral consequence in terms of reaction time when compared to the same task demand in CBA sequences, which also consist of two successive switches, but without returning to a previously inhibited task. Thus, the supplementary cognitive cost for ABA relative to CBA sequences (or “N-2 task-repetition cost”) represents a consequence of backward inhibition and leads to slower reaction time, in addition to the cost of switching itself. This inhibition cost shows that a previously inhibited stimulus dimension is still inhibited (or harder to activate) when it becomes again the relevant dimension (Philipp et al., 2008). In contrast, a “pure” cost of switching can be estimated with a different trial sequence (BBA versus AAA), which only involves the interruption of the previous task-set and the generation of a new, non-inhibited task-set. In the present fMRI study, we used a task switching with these 4 different conditions, allowing us to investigate brain systems recruited by the switching processes, as well as those modulated as a consequence of inhibition.

Studies exploring the neural basis of task-switch have implicated various brain regions, including the prefrontal cortex (Dosenbach et al., 2006; e.g. Luks et al., 2002), pre-supplementary motor area (pre-SMA) (e.g. Rushworth et al., 2002; Woodward et al., 2006), parietal regions (e.g. Forstmann et al., 2006), and basal ganglia (Crone et al., 2006; e.g. Ravizza and Ciranni, 2002), all assembled in a distributed network (Brass and von Cramon, 2004; Dove et al., 2000; Dreher et al., 2002; Pollmann et al., 2000). However, the complexity of paradigms used and the multitude of processes supporting task-switching have hampered definite conclusions (Ravizza and Carter, 2008). Inhibition processes associated with switching have more rarely been studied. The inferior frontal gyrus (IFG) is activated during motor response inhibition (Konishi et al., 1998) but also during switching and other cognitive inhibition demands (Derrfuss et al., 2005; Konishi et al., 1999). This brain region might therefore appear as a good candidate for supporting inhibition in task-switching (Aron et al., 2004; Sakai, 2008), but empirical evidence is still very sparse. One behavioral study in a small sample of frontal damaged patients found a dissociation between the right and left hemisphere respectively for inhibition and activation of task-sets (Mayr et al., 2006). Another study using event-related fMRI compared ABA versus CBA task sequences (Dreher and Berman, 2002) with letter stimuli, and reported that the former type of trials produced greater activation in right lateral prefrontal cortex, as well as left inferior temporal cortex and occipital cortex, possibly reflecting the need of “overcoming inhibition”. On the other hand, to our knowledge, no neuroimaging study so far has investigated the neural bases of the presumed inhibition component during switching, and there is no direct evidence for a “suppression” of specific task-related representations due to such inhibition when switching from one task to another.

In the current study, we aimed at testing the neural consequences of both inhibition and switching processes during a cognitive task with alternating demands. Despite abundant research in behavioral cognitive psychology, the neural substrates recruited and/or modulated by inhibition during task switching remain poorly known. Whereas inhibition of task-related representations has been hypothesized to account for slower response times in ABA than CBA sequences, to our knowledge, there is no empirical evidence to demonstrate that some neural functions are indeed “suppressed” to some degree following the presumed inhibition. Here, using three different judgment tasks with faces, we investigated how previous task inhibition modulated brain activity when returning to the same task and asked whether common or distinctive changes were produced in different task conditions. Thus, we could expect either increased activation in regions previously implicated in cognitive control processes (corresponding to greater “effort” to switch back to the inhibited task-related representations), or reduced activation as a consequence of inhibition (in areas mediating the previously inhibited task-related representations).

In addition, because inhibitory processes might be influenced by emotional signals (Hare et al., 2008; Sagaspe et al., 2011), we also asked whether switching and inhibition would be differentially modulated by emotional information processing. Several studies have reported that emotional cues or emotional states can modulate cognitive control tasks requiring flexibility or shifting abilities (Cohen et al., 2011; Compton et al., 2003; Gray, 2001; Gray et al., 2002; Murphy et al., 2012), suggesting that emotion and executive control may be distinctively connected via brain networks involved in the monitoring of salient information, distribution of attention, and/or selection of appropriate responses (Armony et al., 1997; Compton, 2003). Moreover, the perception of faces and expressions of emotions is an important and particularly efficient ability in humans, guiding social behavior, but also influencing cognitive control and attentional resources in various tasks (Corbetta et al., 2008; Ethofer et al., 2011; Vuilleumier, 2009). Hence, by comparing switching and inhibition in an emotional face condition relative to other non-emotional conditions, our study could also test for neural systems integrating emotion and cognition during task switching, a domain of executive control where affective effects have hitherto not been explored.

For these purposes, we adapted the original paradigm designed by Mayr and Keele (2000) allowing a separate analysis of switching (BBA), inhibition (ABA), and double switch (CBA) conditions, but employing a face categorization task in which three different facial features could be task-relevant (gender, expression, color). We posited that this paradigm should allow us to disentangle the brain substrates recruited during switching (relative to task repetition) and those modulated as a consequence of inhibition (relative to the control condition). First, we predicted that inhibition of task-relevant representations during switching would lead to differential brain activity when returning to the recently inhibited task, as compared with switching to the non-inhibited task. Secondly, we hypothesized that, while the brain networks supporting each task should be different and thus lead to different inhibition effects, common regions associated with attention and executive control might be involved as a result of switching and/or inhibition across the three different tasks. Finally, we also expected that the emotional information might produce differential effects on switching and inhibition at both the behavior and brain activation levels (Compton et al., 2003; Sagaspe et al., 2011).

Material and methods

Participants

Twenty healthy subjects, recruited by advertising and local database, gave informed written consent before inclusion in the study (10 women and 10 men, mean age 24.9 for both gender, std 5.46). All subjects were right-handed as measured by the Edinburgh handedness inventory (Oldfield, 1971), presented no history of previous psychiatric or neurological diseases, and were not taking any medication. Participants filled the Beck Depression Inventory-II (Beck et al., 1996) and the Beck Anxiety Inventory (Beck et al., 1988) in order to exclude potential psychiatric pathologies. Two subjects were excluded due to high scores on these scales (more than 10 points on the BDI). The remaining 18 subjects were included in the neuroimaging analysis. This study was approved by the ethical committee of the Geneva University Hospital.

Apparatus and stimuli

A group of three faces (in a triangle configuration) was presented on the screen. These faces were men or women with an emotional expression (happy or sad) and displayed in red or in green color. Faces could be different in three ways, with either different genders, different emotional expressions, or different color hues (Fig. 1). While gender and emotion are relevant dimensions of facial stimuli, we chose

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