Neuroscience 285 (2015) 227–235

PERFORMANCE MONITORING AND BEHAVIORAL ADAPTATION DURING TASK SWITCHING: AN FMRI STUDY

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Abstract—Despite significant advances, the neural correlates and neurochemical mechanisms involved in performance monitoring and behavioral adaptation are still a matter for debate. Here, we used a modified Eriksen–Flanker task in a magnetic resonance imaging (MRI) study that required the participants to derive the correct stimulus–response association based on a feedback given after each flanker stimulus. Participants had to continuously monitor and adapt their performance as the stimulus–response association switched after a jittered time interval without notice. After every switch an increase of reaction times was observed. At the neural level, the feedback indicating the need to switch was associated with activation of the precuneus, the cingulate cortex, the insula and a brainstem region tentatively identified as the locus coeruleus. This brainstem system appears to interact with this cortical network and seems to be essential for performance monitoring and behavioral adaptation. In contrast, the cerebellum crus and prefrontal areas are activated during error feedback processing. Furthermore we found activations of the hippocampus and parahippocampal gyrus bilaterally after a correct feedback in learnable stimulus–response associations. These results highlight the contribution of brainstem nuclei to performance adaptation.

Key words: locus coeruleus, ACC, hippocampus, task switching, performance monitoring, fMRI.

INTRODUCTION

In order to achieve internal goals most effectively humans are required to adapt their behavior continuously to changing environmental demands (Allport et al., 1994). Accordingly, the ability to shift flexibly between different task sets is an essential prerequisite. The term task set refers to the configuration of mental resources comprising the representation of task-relevant stimuli, task-relevant responses, and the corresponding stimulus–response mapping (Kiesel et al., 2010). At the behavioral level, a switch between different task sets results in increased reaction times and/or error rates, an effect that is known as switch costs (Jersild, 1927). These "switch-costs" are evident from the comparison of switch and task repeating trials (Monsell, 2003; Kiesel et al., 2010). It is assumed, that switch-costs are caused by proactive interference from previous tasks (Yeung et al., 2006) and by task-set reconfiguration processes (Monsell, 2003). Task-set reconfiguration processes are time consuming preparation processes like the backward inhibition of the previous task set, the overcoming of the now relevant task set's inhibition (Mayr and Keele, 2000), attention shifting between stimulus attributes, and the encoding or deleting of stimulus–response associations in working memory (Monsell, 2003), that are necessary to enable appropriate behavioral adaption to a task set switch.

At the neural level, imaging but also lesion studies in monkeys (Rushworth et al., 2003; Kovach et al., 2012) identified a fronto-parietal network to be relevant for task switching related processes. This network includes the dorsal ACC (anterior cingulate cortex) for conflict monitoring (Mars et al., 2005; Hyafil et al., 2009; Ide et al., 2013), the superior parietal lobule for attentional control (Braver et al., 2003), the lateral prefrontal cortex and intraparietal sulcus for implementation of task goals (Brass and von Cramon, 2004; Hyafil et al., 2009) the pre-SMA (supplementary motor area), inferior parietal lobule and middle temporal gyrus for task-set preparation (De Baene and Brass, 2013) and the pre-SMA and basal ganglia for the inhibition of previous task sets (Whitmer and Banich, 2012). Furthermore, the anterior insular cortex has been suggested to be involved in error awareness (Bush et al., 2000; Klein et al., 2007; Ullsperger et al., 2007) and is assumed to be active in case a task switch fails.

There is increasing evidence for an involvement of the noradrenergic system in task switching behavior by regulating arousal and cognitive flexibility (Lapish et al., 2007; Jocham and Ullsperger, 2009). The main source of noradrenaline is the locus coeruleus (LC), a group of neurons located in the brainstem, which projects to the prefrontal cortex, where the modulating function of the noradrenergic system on behavioral flexibility and attentional shifting might manifest (Devauges and Sara,

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Abbreviations: ACC, anterior cingulate cortex; ANOVA, analysis of variance; EPI, echo planar imaging; IR-EPI, inversion recovery echo planar imaging; LC, locus coeruleus; MRI, magnetic resonance imaging; SMA, supplementary motor area.

http://dx.doi.org/10.1016/j.neuroscience.2014.11.024

1990; Aston-Jones and Cohen, 2005; Bouret and Sara, 2005; Yu and Dayan, 2005; McGaughy et al., 2008; Sara and Bouret, 2012). Some studies already investigated the response of noradrenergic neurons in typical situations (Aston-Jones and Cohen, 2005; Sara, 2009; Sara and Bouret, 2012): During quiet wakefulness, LC neurons are in a tonic mode, firing at a regular slow rate. With the appearance of a behaviorally significant stimulus they shift to a phasic mode, firing short-latency bursts. This phasic mode is associated with focused attention to the stimulus and optimization of behavioral performance, like switching the stimulus–response association (Aston-Jones and Cohen, 2005). Whenever the behavioral relevance of a task wanes, LC neurons fall back to the slow firing rate of the tonic mode, which is at a cognitive level associated with a disengagement from the task.

An increased availability of prefrontal noradrenaline induced by drug treatment (Arnsten, 2006a,b; Devilbiss and Berridge, 2008; Lin et al., 2009) or via the firing of the LC is reported to increase cognitive flexibility (Usher et al., 1999; Allen et al., 2005; Aston-Jones and Cohen, 2005; Bouret and Sara, 2005; Cain et al., 2011). Indeed, lesion studies in animals (McGaughy et al., 2008; Tanaka et al., 2009) as well as drug treatments (Lapiz and Morilak, 2006; Cain et al., 2011; Brown et al., 2012) revealed a positive relationship between noradrenaline availability and improved set shifting. In humans, a similar impact of drug treatments affecting the noradrenaline system on task switching behavior was described (Renner and Beversdorf, 2010; Demanet et al., 2011; Chamberlain and Robbins, 2013). The drug Modafinil elevates the synaptic noradrenaline and dopamine level and enhances the phasic response of LC to task-relevant events while tonic LC activity is decreased (Hou et al., 2005; Minzenberg et al., 2008) leading to an increase of prefrontal cortex activity and an improved task performance (Minzenberg et al., 2008). Moreover, manipulating the noradrenaline system has been shown to increase performance accuracy. For instance, Riba et al. (2005) reported that stimulating noradrenergic transmission via the application of the alpha-adrenoceptor antagonist yohimbine results in an improvement of performance accuracy in an Eriksen–Flanker task.

The present study aimed to investigate the interaction of the neural systems involved in task switching and performance monitoring. Since action monitoring is known to rely primarily on projections of the mesolimbic dopaminergic system, we expected brain sites belonging to the dopaminergic (action monitoring) as well as the noradrenergic system (task switching) to be active. Participants had to perform a modified Eriksen flanker task, in which the valid stimulus–response association changed without informing the participant while functional magnetic resonance imaging (MRI) was recorded. Participants were able to detect a task switch via a symbolic feedback that was given after each response, informing the participant if the given response was correct regarding the valid task set. In case a task set switch took place, participants received the feedback of having responded incorrectly, although their response was correct in terms of the previously valid task set. Accordingly, subjects had to be sure regarding their performance quality in order to detect a task set switch. We expected activation of the LC in response to the switch feedback in light of the literature indicating a role of the noradrenaline system in task switching. Furthermore, we expected to see an activation of the performance monitoring network including the anterior cingulate gyrus.

EXPERIMENTAL PROCEDURES

The experimental procedures had been approved by the local ethics committee prior to the experiment. All experiments were carried out according to the declaration of Helsinki.

Participants

After obtaining informed written consent, sixteen healthy volunteers (nine men, seven women) participated in this study. All participants were right-handed and were between 20 to 26 years old (mean age: 23.06 years). All participants were paid for their participation (7 Euros/hour).

Experimental procedure

For the Eriksen–Flanker task (Eriksen and Erkisen, 1974) five letter-strings consisting of ''H'' and ''S'' were used as congruent (HHHHH, SSSSS) and incongruent stimuli (HHSHH, SSHSS). These stimuli were presented in a random order with incongruent stimuli in 60% of all trials to increase the task's difficulty. Participants were instructed to respond to the central letter by button-press with either the index or the middle finger. In contrast to other studies, participants were not informed about a fixed stimulus–response association. Instead, they had to figure out the currently valid stimulus–response association via a feedback stimulus, which was presented after each flanker stimulus. This feedback stimulus consisted of a colored square, which was green in case the response was correct and red after an incorrect button press. After a jittered interval (every 6th to 11th trial) the stimulus–response combination was switched (switch trial). The subjects were not explicitly informed about this switch but had to derive the new task set from the feedback. Thus, an index finger response to an H might have been appropriate for the trial preceding the switch, resulted in a red square feedback after the switch. Obviously, subjects were only able to interpret a red square as a signal to switch the task set, when they were sure to have responded correctly. In the following we name the first red square feedback after a switch ''switch feedback''. In contrast, a red square feedback after an incorrect button press is called ''error feedback''. Participants were instructed to respond as fast as possible. If the response time exceeded a deadline of 1 s a feedback comprising a gray square was given (Fig. 1). We choose the Flanker task because it is an easy task with only two stimulus–response associations which produces a fair amount of performance errors, which allows us to show the difference between performance and switch errors.