NeuroImage 63 (2012) 1552–1560

Contents lists available at SciVerse ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

Context-dependent switching between proactive and reactive working memory control mechanisms in the right inferior frontal gyrus

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ARTICLE INFO

Article history:
Accepted 6 August 2012
Available online 11 August 2012

Keywords:
Working memory
Executive control
Functional magnetic resonance imaging (fMRI)
Inferior frontal gyrus (IFG)
Proactive
Reactive

ABSTRACT

A critical feature of higher cognitive functioning is the capacity to flexibly tailor information processing and behaviors to current situational demands. Recent neurocognitive models have been postulated to account for the dynamic nature of human executive processing by invoking two dissociable cognitive control modes, proactive and reactive control. These may involve partially overlapping, but temporally distinct neural implementation in the prefrontal cortex. Prior brain imaging studies exploring proactive control have mainly used tasks requiring only information about single-items to be retained over unfilled delays. Whether proactive control can also be utilized to facilitate performance in more complex working memory tasks, in which concurrent processing of intervening items and updating is mandatory during contextual cue maintenance remains an open question. To examine this issue and to elucidate the extent to which overlapping neural substrates underlie proactive and reactive control we used fMRI and a modified verbal 3-back paradigm with embedded cues predictive of high-interference trials. This task requires context information to be retained over multiple intervening trials. We found that performance improved with item-specific cues predicting forthcoming lures despite increased working memory load. Temporal dynamics of activation in the right inferior frontal gyrus suggest flexible switching between proactive and reactive control in a context-dependent fashion, with greater sustained responses elicited in the 3-back task involving context maintenance of cue information and greater transient responses elicited in the 3-back task absent of cues.

Introduction

Attaining behavioral goals require executive control mechanisms important for selecting task-relevant information and suppressing task-irrelevant information. A large body of cognitive and neuroscience research have focused on defining the variety of subprocesses by which executive control guides behavior, and the brain structures upon which these functions depend. Core regions involved in executive control constitute the lateral PFC, the anterior cingulate cortex (ACC), basal ganglia and brainstem neuromodulatory systems (e.g. Duncan and Owen, 2000; Marklund et al., 2007; Nyberg et al., 2003). However, the specific functional contribution of these regions and their interactive role in the coordination of cognitive processes still remains to be well characterized. In a recent theoretical framework, the dual mechanisms of control (DMC) model, Braver and co-workers have proposed two dissociable but complementary control modes, referred to as proactive and reactive control, to account for the dynamic nature of human executive processing (e.g. Braver et al., 2007, 2009). According to DMC a fundamental distinction among diverse executive functions can be inferred from the temporal signature of their neural implementation in task-relevant circuitry.

Proactive control mechanisms reflect tonic preparatory processes that rely on active maintenance of goal-relevant context information, exerting their mitigating effect on behavioral conflict/interference in a pre-stimulus manner or across entire task blocks. This “early selection” mode is associated with sustained neural activity and appears to be obligatorily triggered by cue-induced expectation of changes (i.e., augmentation) in processing demand on the next trial(s) (e.g., cued task-set switching) but may in principle carry any context information conveying a facilitatory bias on future response selection. By contrast, reactive control mechanisms operate on a trial-to-trial basis and remain dormant until ‘online’ detection of conflict triggers this “late correction” mode associated with episodic retrieval or reactivation of context and transient neural activity (Braver and West, 2008).

Because of the great expenditure of neural resources invested to maintain a tonic mode of preparatory attention, proactive control is conjectured to be mainly deployed in situations defined by high expectancy

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1053-8119/$ – see front matter
http://dx.doi.org/10.1016/j.neuroimage.2012.08.016

with respect to need for PFC-mediated executive processing to overcome impending conflict (Braver et al., 2007). In keeping with this notion, a recent study manipulating interference expectancy during a working memory task, demonstrated an expectancy-dependent shift from transient probe-related activity to sustained preparatory activity in the left lateral PFC regions (Burgess and Braver, 2010). Proactive control may also be engaged in situations when there are large behavioral consequences or motivational benefits for accurate performance (e.g. Jimura et al., 2010; Locke and Braver, 2008).

The less resource-demanding reactive control mode is preferred in situations where it is difficult to foresee conflict and when available resources are running low (e.g., in elderly relative to young adults) (Paxton et al., 2008) for individuals low in working memory capacity (Burgess and Braver, 2010), and when task demands reach or surpass the limits of working memory capacity (Speer et al., 2003). In a similar vein, another theoretical model of executive control, proposed by Kane and colleagues (e.g. Kane et al., 2004), suggests that active maintenance of task relevant goals (proactive control) becomes crucial primarily when demands on overcoming interference are high, but only to the degree that individuals are endowed with high working memory capacity, and interference can be anticipated. Otherwise, they posit that reactive-like inhibitory processes need to be engaged to overcome trial-specific interference. For consistency we will be referring to these two control strategies as proactive and reactive executive control.

The requirements on PFC-mediated executive control needed to guide behavior are not only upregulated by the presence of task-irrelevant information competing with task-relevant information, but also to the extent that concurrent task-relevant processing impinges upon shared limited executive resources. Prior investigations aimed at elucidating the neural mechanisms of proactive control employed rather unchallenging tasks in this respect, such as cued-task switching (Braver et al., 2003; Ruge et al., 2009), AX-CPT (Paxton et al., 2008), and the recent probes task (Burgess and Braver, 2010). In these tasks, the executive load imposed on preparatory attention via context maintenance is rather small. For example, in the AX-CPT, only information about the most recently encountered item (whether 'X' or not 'X') must be retained over unfilled delays to guide upcoming responses.

The extent to which the same type of proactive control mechanisms can be utilized to anticipate and prepare for interference or conflict resolution, and ultimately, facilitate performance, when task demands are more stringent and entail other executive processes besides context maintenance that likely compete for the same neurocognitive resources, remains to be determined. In light of the prediction from DMC that lateral PFC regions in a domain-general common executive network should be capable of flexibly shifting between operational modes (Braver, 2012), it is of key theoretical interest to investigate whether resource-demanding proactive control is still amenable in more complex working memory tasks known to rely on the same neural substrates, putatively constraining available resources for context maintenance. Toward this end, the present fMRI study used two variants of the 3-back task. Participants performed both a conventional 3-back task (uncued task condition), which stresses reactive control, and a modified version (cued task condition) with embedded cues predictive of forthcoming high-interference trials requiring contextual information to be retained over multiple intervening trials, which should promote proactive control. However, even if high expectancy of conflict is critical for adopting a proactive mode (Braver et al., 2007), maintaining such explicit cues also increase the burden on working memory, which is already high in 3-back, and thus tentatively discourage utilization of proactive control.

Using a mixed blocked/event-related design (e.g. Donaldson et al., 2001; Petersen and Dubis, 2012; Visscher et al., 2003) we investigated: 1) potential facilitatory behavioral effects of predictive cue information on high-interference resolution in tasks involving substantial working memory load, and 2) whether we could find regions implied in domain-general executive control (specifically lateral PFC) exhibiting the inverse pattern of activity dynamics when directly comparing transient and sustained neural responses, respectively, between the two 3-back task conditions. The idea is that such regions, demonstrating relatively greater sustained activity in the cued 3-back task (indexing proactive control) together with relatively greater transient activity in the uncued 3-back task (indexing reactive control), would indicate a unitary adaptive control mechanism underlying proactive and reactive control processes. Regions showing this pattern would be critical for high-interference resolution, with the mode of operation switching flexibly in a context-dependent fashion to optimize performance.

Methods

Participants

Thirty young adults (22 males; age range: 18–30 years) were recruited from the Umeå University community through posted advertisements. They all gave informed consent, were native Swedish speakers and had normal or corrected to normal vision. The investigation was approved by the Ethics Committee in Stockholm. Eight participants were excluded from the fMRI analyses because of technical problems and poor image quality arising from movement artifacts. Participants first completed a health screen over the telephone to ensure their suitability for the study. The fMRI scanning took place at the MRI Research facility where participants were given task instructions and completed practice versions of each of the tasks before the start of the scanning protocol.

fMRI task

We used the N-back paradigm, which has been frequently used in neuroimaging studies assessing maintenance and updating processes in working memory. A total number of 224 words were partitioned into 16 task blocks (8 cued-interference and 8 uncued task blocks). Each word was presented for 2000 ms in a sequential order, with a uniform distribution of jittered interstimulus intervals at 500, 2500, 5000, and 7500 ms. The total time for performing the task was 18 min. Participants pressed the left button as quickly and accurately as possible when a word matched the one presented three words earlier, and the right button if the word had not been presented three words earlier. Thirty-six of the words matched the earlier item (target trials), and 188 did not (non-target trials). Here we use an interference version of the task (see also Derrfuss et al., 2004; Gray et al., 2003), in which target trials were intermixed with different kinds of non-target trials. On three quarters of the non-target trials the word presented matched the word two or four trials previously; thus, increased familiarity of a word due to its recent exposure (and hence increased demands for interference resolution). These non-target words were classified as lures. On the remaining non-target trials, the word presented was not a lure (i.e. an item not previously presented).

Importantly, we used two variants of this task (Fig. 1); a standard verbal 3-back task that was used for assessing reactive control, and a modified "cued" interference version that was designed to encourage participants' use of a proactive strategy. This was done by embedding item-specific contextual cues (i.e. lure words were tagged with a "2" or "4" during their initial presentation) to disclose 2- and 4-back high interference probes in advance. For all other stimuli, both target items and never repeated lures, were tagged with an uninformative "0". This enables advance preparation using proactive control for a negative response on high-interference trials (i.e. 2- and 4-back lures). Such preparation was not possible in the uncued N-back condition where an uninformative "0" was presented, and participants need to engage in reactive control mechanisms in order to resolve interference from the familiar, but not task-relevant stimuli. Using a hybrid fMRI-protocol with jittered stimulus presentation allowed us to tease apart, and directly compare sustained and transient (stimulus-