Neuroscience and Biobehavioral Reviews 46 (2014) 58–70

Contents lists available at ScienceDirect

Neuroscience and Biobehavioral Reviews

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

Review

Mechanisms and neuronal networks involved in reactive and proactive cognitive control of interference in working memory

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ARTICLE INFO

Article history:
Received 2 September 2013
Received in revised form 22 June 2014
Accepted 27 June 2014
Available online 6 July 2014

Keywords:
Decision making
Interference in working memory
Proactive cognitive control
Reactive cognitive control

ABSTRACT

Cognitive control can be reactive or proactive in nature. Reactive control mechanisms, which support the resolution of interference, start after its onset. Conversely, proactive control involves the anticipation and prevention of interference prior to its occurrence.

The interrelation of both types of cognitive control is currently under debate: Are they mediated by different neuronal networks? Or are there neuronal structures that have the potential to act in a proactive as well as in a reactive manner? This review illustrates the way in which integrating knowledge gathered from behavioral studies, functional imaging, and human electroencephalography proves useful in answering these questions. We focus on studies that investigate interference resolution at the level of working memory representations. In summary, different mechanisms are instrumental in supporting reactive and proactive control. Distinct neuronal networks are involved, though some brain regions, especially pre-SMA, possess functions that are relevant to both control modes. Therefore, activation of these brain areas could be observed in reactive, as well as proactive control, but at different times during information processing.

Contents

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http://dx.doi.org/10.1016/j.neubiorev.2014.06.014
0149-7634/

1. Introduction

Decision making is dependent on the ability to exert cognitive control over reflexive and habitual responses (Miller, 2000). Cognitive control is assumed to consist of multiple components (e.g. Badre and Wagner, 2007; Banich et al., 2000; Parks and Madden, 2013). One influential theory, the dual mechanisms of control (DMC) theory (Braver et al., 2007, 2009; Braver, 2012; De Pisapia and Braver, 2006), differentiates between a reactive and a proactive control mode with distinct temporal dynamics. In the reactive control mode, control processes are recruited as late correction mechanisms, for instance after detection of interference between automatic and controlled responses. In the proactive control mode, goal-relevant information is actively maintained in an anticipatory manner over a period of time, even before the occurrence of a cognitively demanding event or before the registration of a conflict between reflexive and controlled behavior. Thus, proactive control aims to minimize interference from internal or external sources on decision making, whereas reactive control aims to reduce the effect of interference on the decision making process after its detection.

Both modes also differ with regard to the effort and the attentional commitment required, which explains the benefits and disadvantages of either strategy, depending on the frequency and expectancy of the cognitively demanding event. Proactive control consumes resources and implements a form of sustained mental set that reduces sensitivity to unexpected but potentially relevant sources of information. Reactive control requires a retrieval or activation of goal representations only at the time at which they are needed, and is therefore computationally efficient. On the other hand, it is late acting and stimulus-dependent, and efficiency depends on the saliency of the stimulus and on the strength of associated cues that enable the retrieval of stored goals. The brain is able to shift flexibly between both modes according to task demands (Braver, 2012).

In this framework, *intra*-individual variability regarding the preferred cognitive control strategy results from a change in situational factors, like interference expectancy (Burgess and Braver, 2010). *Inter*-individual differences are explained by factors like working memory capacity, fluid intelligence (Burgess and Braver, 2010), aging (Paxton et al., 2008), and personality factors, such as reward sensitivity. These factors influence the value estimates of the relative benefits and disadvantages of the preferred mode of control (Jimura et al., 2010).

The DMC theory is applicable in interpreting findings from different paradigms and domains in the research of cognitive control, such as behavioral switching, task-switching, interference in working memory, Stroop task, n-back task and Go/Nogo task (e.g. Czernochowski et al., 2010; Grandjean et al., 2012; Marklund and Persson, 2012; Ullsperger and King, 2010; West and Bailey, 2012).

The neuronal interrelation of both types of cognitive control is currently under debate: Are they mediated by different neuronal networks? Or are there neuronal structures that have the potential to act in a proactive as well as in a reactive manner? The DMC account predicts that proactive control should be associated with *sustained* and/or anticipatory activation of the lateral prefrontal cortex (PFC), whereas reactive control *transiently* involves the lateral PFC, and activates, either via detection of interference (through engagement of conflict monitoring regions such as anterior cingulate cortex (ACC)), or via associative and episodic associations, the posterior or medial temporal lobe regions (Braver, 2012).

This review illustrates the way in which the integration of knowledge gathered from behavioral studies, functional imaging with its high spatial resolution and human electroencephalography with its high temporal resolution proves useful in answering the following questions: What is known about the mechanisms underlying proactive and reactive control, and is it conceivable that they are independent from one another? Are they mediated by different neuronal networks? Or are there neuronal structures that have the potential to act in a proactive as well as in a reactive manner? The DMC theory proposes that the ACC plays a role in the proactive as well as the reactive control networks. Others, like Ullsperger and King (2010) suggest a dichotomy of medial frontal regions (pre-supplementary motor area (pre-SMA) and ACC) in the sense that ACC is involved in reactive control, whereas pre-SMA is activated in proactive cognitive control, regardless of the level of information processing at which conflict occurs. The medial frontal cortex is thought to play an important role in regulating cognitive control and different theories postulate its involvement in conflict monitoring (e.g. Botvinick et al., 2001, 2004; Carter and van Veen, 2007), prediction of task difficulty or error likelihood (Brown and Braver, 2005; Carter et al., 1998; Nieuwenhuis et al., 2007) or reward-based decision-making (see for instance Hayden and Platt, 2010). Is there evidence supporting the hypothesis of a dichotomy of medial frontal cortex regions, as suggested by Ullsperger and King (2010)? To answer these questions, we focus mainly on studies investigating interference resolution at the level of verbal working memory representations, because neuronal networks and mechanisms involved in cognitive control of conflict or interference seem to be, at least partially, dependent on the material (e.g. Badre and Wagner, 2005; Leung and Zhang, 2004; Mecklinger et al., 2003) and the level of information processing at which conflict occurs (see for instance Bisset et al., 2009; Friedman and Miyake, 2004; Nee and Jonides, 2008; Nelson et al., 2003). It has to be taken into account that the general question of a dichotomy of medial frontal cortex regions in cognitive control is addressed here with only one specific requirement as verbal working memory. Therefore, it allows no statement regarding cognitive control in other task domains, such as inhibitory motor control or task switching. On the other hand, working memory plays an integral role in most forms of intelligent behavior (Nee et al., 2007), and capacity differences are related to differences in intelligence, reasoning, reading comprehension and problem-solving (Cowan et al., 2005; Daneman and Merikle, 1996; Just and Carpenter, 1999).

A major factor in determining the capacity of short-term memory is the ability to protect it against interference from previously relevant information. Therefore, interference resolution at the level of working memory representations was intensively studied in recent years and a wealth of neuropsychological, functional imaging, electrophysiological, and lesion studies were performed to identify the mechanisms and neuronal networks involved.

In the following section, the concept of interference in working memory is introduced.

Thereafter, mechanism and networks involved in reactive and proactive control are presented and discussed separately.