



The impact of mental workload on inhibitory control subprocesses



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ARTICLE INFO

Article history:

Accepted 26 February 2015

Available online 6 March 2015

Keywords:

Inhibitory control
Working memory
NoGo-N2
NoGo-P3
Prefrontal cortex

ABSTRACT

The inhibition of inappropriate responses is a function known to rely on prefrontal cortex (PFC) functioning. Similarly, working memory processes are known to rely on the PFC. Even though these processes are usually closely intertwined and the functional neuroanatomy underlying these processes is largely overlapping, the influence of working memory load on inhibitory control process has remained largely elusive. In the current study, we therefore examine how response inhibition processes are modulated by working memory load. For this, we systematically increased the working memory load of participants by integrating mental rotation processes in a Go/NoGo paradigm. To examine the system neurophysiology of these processes in detail, and to examine whether there are differential effects of working memory load on distinct response inhibition subprocesses, we applied event-related potentials (ERPs) in combination with source localization techniques. The data shows that after exceeding a certain threshold, inhibitory control processes are aggravated by working memory load. The neurophysiological data paralleled the behavioral data. However, it suggests that distinguishable response inhibition subprocesses are differentially modulated by working memory load: Changes were evident in the NoGo-P3 amplitude but not in the NoGo-N2 amplitude. On a system level, this distinctive modulation of response inhibition subprocesses was related to differences in neural activity in the left inferior and middle frontal gyri. We show that inhibitory control processes are impaired when the working memory load surpasses a certain threshold. This, however only applies to situations in which the necessity of inhibitory control processes cannot be easily detected on the basis of perceptual factors.

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Introduction

When attempting to master a task, different executive functions are required. One of them, namely inhibitory control (Bari and Robbins, 2013; Diamond, 2013), is crucial for blocking inappropriate responses. Others, like working memory (Baddeley, 1992; Baddeley and Hitch, 1974; Diamond, 2013), are a limiting factor, since only a certain capacity is available for the maintenance and processing of information that is used to perform response inhibition processes, for example. Even though these two factors are closely intertwined in daily life, it has remained widely elusive in how far increasing working memory load impacts response inhibition processes and in how far there are distinctive effects on dissociable response inhibition subprocesses that can be examined using neurophysiological (EEG) techniques. In the current study, we therefore examined these questions by systematically modulating working memory load and examining its effects on response inhibition processes.

Traditionally, inhibitory control processes are often examined using Go/NoGo tasks (Beste et al., 2011; Casey et al., 1997; Nieuwenhuis et al.,

2003; Ocklenburg et al., 2013; Rubia et al., 2001; Stock et al., 2014). In these paradigms, stimulus–response contingencies that trigger largely automatized reactions are established. These pre-potent response tendencies however have to be overcome in a subset of trials, thus challenging participants to actively inhibit the intended reactions. From a system level perspective, a distributed prefrontal network is assumed to mediate these response inhibition processes (Aron et al., 2003, 2004; Chamberlain et al., 2009; Chikazoe et al., 2007; Garavan et al., 1999; Hampshire et al., 2010; Munakata et al., 2011). In this network, PFC activity is assumed to reflect goal maintenance as it represents and maintains abstract information required for successful inhibition (Munakata et al., 2011). According to Braver and Barch (2002), response inhibition and working memory processes might both rely on top-down strengthening of task-relevant representations; i.e. the strengthening of the representation of the correct response, or respectively of task-relevant information. In this regard, response inhibition mechanisms rely upon functional neuroanatomical structures and processes that are also central for working memory functions (Barch et al., 1997; Cohen et al., 1997; Curtis and D'Esposito, 2003; D'Esposito et al., 2000). To examine working memory processes in the visual domain, mental rotation paradigms have been established (Hyun and Luck, 2007; Kaufman, 2007; Shepard and Metzler, 1971, 1988). When applying these paradigms, it has been shown that on a functional neuro-anatomical level, parietal and frontal areas are essential for mental

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rotation processes as a means to examine visual working memory (Alivisatos and Petrides, 1997; Cohen et al., 1996; Jordan et al., 2001; Kosslyn et al., 1998; Zacks, 2008). Especially in the inferior frontal gyrus (IFG), increased activity can be observed whenever workload is increased (Jaeggi et al., 2007; Leung and Cai, 2007; Michael et al., 2001). Considering the functional anatomical overlap of mental rotation (visual working memory) and response inhibition processes, it appears likely that response inhibition processes are modulated by systematically increasing visual working memory load, as induced by mental rotation requirements. In line with that hypothesis, it has been shown that increased task difficulty induces an aggravation of inhibitory control processes, even though the exact mechanisms have not been stated (Vaurio et al., 2009; Wodka et al., 2007). Previous studies examining the interrelation of working memory and response inhibition processes examined this interrelation on a behavioral level (e.g. Grandjean and Collette, 2011), or used functional magnetic imaging techniques (e.g. Mostoksky et al., 2003; Barber et al., 2013). While all these studies speak for an interrelations of working memory and response inhibition processes it is unclear what response inhibition sub-processes are mostly affected by the manipulation of working memory load.

To examine in how far working memory load differentially affects response inhibition subprocesses, we examined neurophysiological data (event-related potentials, ERPs) and performed source localization analyses. Using ERPs, it is possible to distinguish between two response inhibition subprocesses that are possibly differentially affected by mental workload. These subprocesses are reflected by two event-related potentials (ERPs), namely the fronto-central negative-positive N2–P3 complex (Beste et al., 2010b; Bokura et al., 2001; Falkenstein et al., 1999; Huster et al., 2013; Lavric et al., 2004; Smith et al., 2010). While the NoGo-N2 is assumed to reflect pre-motor inhibition processes (i.e. the inhibition or revision of a motor plan/program before the actual motor process, see Beste et al., 2010b; Falkenstein et al., 1999; Jodo and Kayama, 1992; Lavric et al., 2004), the NoGo-P3 is assumed to either reflect the act of inhibition itself (Beste et al., 2010b; Falkenstein et al., 1999; Huster et al., 2013; Schmajuk et al., 2006), a stimulus evaluation process (Friedman et al., 2001), or the inhibition outcome evaluation (Schmajuk et al., 2006). Aside from these two ERPs, we also examined the rotation-related negativity to illuminate the impact of inhibitory control processes on mental rotation processes. The rotation-related negativity can be observed in mental rotation tasks and is thought to reflect the angular displacement of the stimulus material (Bajric et al., 1999; Band and Kok, 2000; Beste et al., 2010a; Heil and Rolke, 2002; Koshino et al., 2005).

We assumed inhibitory control processes and mental rotation processes to be interdependent processes. We therefore hypothesize that inhibitory control processes are aggravated by systematically increasing workload; i.e. that a stepwise increase of the rotation angle will lead to an increasing frequency of false alarms. Along with that, we hypothesized that the NoGo-N2 and NoGo-P3 show a decrease in their amplitudes as a correlate of less efficient response inhibition under increasing working memory load. However, we expected that NoGo-P3 processes are more affected than NoGo-N2 processes, because processes reflected by the NoGo-P3 occur in a time window in which also mental rotation processes lead to a workload-dependent modulation of neurophysiological responses. Since the IFG is involved in response inhibition and working memory processes, we furthermore assumed the increase of working memory load on inhibitory trials to be reflected in IFG activity. Moreover, we assumed a reversed pattern to be observable in the rotation-related negativity. Since the employed task required mental rotation processes to determine whether or not inhibitory control processes are necessary, we expected the rotation-related negativity to increase with increasing rotation angle on inhibitory trials. In case the necessity of inhibitory control processes is easily detectable, we also assumed the rotation-related negativity to be decreased due to a resulting cancellation of the mental rotation process.

Material and methods

Participants

A total of $n = 25$ healthy young participants (17 females) between 18 and 30 years old (mean age 25 ± 2.6) took part in the experiment. All participants had normal or corrected vision, were free of medication and reported no psychiatric or neurological disorders. Before the test protocol was conducted, written informed consent was obtained from all participants. The study was approved by the institutional review board of the Medical faculty of the TU Dresden and realized in accordance with the Declaration of Helsinki.

Task

For the task employed in this study, rotated numbers and characters were used as stimuli in a Go/NoGo paradigm. To ensure the classic characteristics of a Go/NoGo task, 30% NoGo trials requiring no response and 70% Go trials that required a specific response by the participants were utilized. The characters G and R and the numbers 5 and 7 were employed as target stimuli due to their good visual discriminability and due to the fact that these stimuli are known to not evoke sex-dependent differences in the mental rotation process (Jansen-Osmann and Heil, 2007). By means of target rotation, varying working memory load was induced in this Go/NoGo paradigm. Equal proportions of each target stimulus were rotated by 30, 90, or 150°, thus evoking an increasing workload from the smallest to the largest rotation angle (Band and Kok, 2000; Koshino et al., 2005). Targets were presented rotated clockwise and counter-clockwise in a normal (not mirrored) and a mirrored fashion (Beste et al., 2010a; Heil, 2002; Heil et al., 1998).

To thoroughly examine the impact of workload on response inhibition, two blocks with alternating task complexity/difficulty were created. As mentioned above, numbers and letters were chosen as targets, thus establishing two target categories (numbers vs. letters) that can easily be distinguished. In the less demanding block A, all letters required a response, thus constituting the Go stimulus category. In contrast, all numbers required no response, thus constituting the NoGo stimulus category. Thus, NoGo trial processing was facilitated based on perceptual information (letter vs. number). In other words, as soon as the target was identified as a number, mental rotation of the stimulus could be canceled for these NoGo trials. On Go trials in block A, the presentation of a mirrored letter required a button press with the left hand, while the presentation of a normal (not mirrored) letter required a right hand response. In contrast to block A, numbers and letters were utilized as targets in the more challenging block B. Here, task complexity/difficulty was increased in comparison to block A, because participants could no longer benefit from the category information (letter vs. number). In this block, responses had to be carried out to un-mirrored targets, while mirrored numbers or letters required no response and thus served as NoGo trials. It was therefore necessary to perform mental rotation processes in order to decide whether or not to respond. These mental rotation processes increase working memory load, thus allowing to examine the influence of mental workload on response inhibition processes. As both blocks A and B required a response to normal, un-mirrored letters, transfer effects between the two blocks needed to be ruled out. To do so, normal, un-mirrored letters required a left hand response in block B (as compared to a right-hand response in block A). Consequently, the presentation of normal, un-mirrored numbers required a right hand response in block B. In order to provoke inhibition errors and to further amplify the effect of workload manipulation through time pressure, participants were generally requested to respond as fast and accurately as possible in each trial during the whole task.

Each trial began with an 800 ms presentation of a fixation cross, which was followed by a 1100 ms target presentation. Irrespective of

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