



Complementary roles of cortical oscillations in automatic and controlled processing during rapid serial tasks



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ARTICLE INFO

Article history:

Accepted 28 May 2015

Available online 3 June 2015

Keywords:

MEG

Response inhibition

Response selection

Frontal theta

Sensorimotor gamma

SART

ABSTRACT

Cognitive control may involve adjusting behaviour by inhibiting or altering habitual actions, requiring rapid communication between sensory, cognitive, and motor systems of the brain. Cognitive control may be achieved using top-down processing from frontal areas to inhibit prepared responses, likely mediated through frontal theta (4–8 Hz) oscillations. However there is conflicting evidence for mechanisms of response inhibition, where global and selective inhibition are either considered separate processes, or frontal areas maintain and execute goal-directed actions, including inhibition. In the current study we measured neuromagnetic oscillatory brain activity in twelve adults responding to rapidly presented visual cues. We used two tasks in the same subjects that required inhibition of a habitual “go” response. Presentation of infrequent “target” cues required subjects to completely inhibit responding (go/no-go task) or to perform an alternate response (go/switch task). Source analysis of oscillatory brain activity was compared for correct no-go and switch trials as well as error trials (“go” responses to targets). Frontal theta activity was similar in cortical location, amplitude and time course for correct no-go and switch responses reflecting an equivalent role in both global and selective response inhibition. Error-related frontal theta activity was also observed but was different in source location (errors vs correct, both tasks: $p < 0.005$) and power (go/switch > go/no-go error, correct switch power, $p = 0.01$). We additionally observed sensorimotor high gamma (60–90 Hz) activity accompanying motor responses, which was markedly stronger for correct switch and error responses compared with go responses, and was delayed for errors ($p < 0.01$). These results suggest that gamma signals in the motor cortex may function to integrate inhibitory signals with sensorimotor processing, and may represent a mechanism for the overriding of habitual behaviours, as errors were predicted by a delay in gamma onset. This study supports a role for frontal areas in maintaining and executing goal-directed actions, and demonstrates that frontal theta activity and sensorimotor gamma oscillations have distinct yet complementary functional roles in monitoring and modifying habitual motor plans.

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Introduction

A longstanding interest in neuroscience has been the coordination of behaviour under conditions of competing task demands. Of particular interest in the present paper is our ability to efficiently select between a high frequency habitual response and a rare alternative, which may involve either simply inhibiting the habitual response or selecting an alternative response. It is thought that inhibitory control is achieved using top-down processing from frontal areas that override prepared motor

programs, however there is conflicting evidence for the underlying mechanisms. There is evidence for a distinction between global and selective inhibitory processes (De Jong et al., 1990, 1995), however there is also substantial evidence that frontal areas simply maintain and execute goal-directed actions, including inhibition (Band and van Boxtel, 1999; Collette et al., 2005; Criaud and Boulinguez, 2013; Jasinska, 2013; Kenner et al., 2010; Miller and Cohen, 2001; Munakata et al., 2011), with a prominent role for frontal theta (4–8 Hz) oscillations (Cavanagh and Frank, 2014). In the current study we compare a task of complete response inhibition with a task of switching to an alternate response instead. The purpose is to compare frontal theta oscillations across tasks, where observations of different theta activity would indicate a frontal source for the distinction in global and selective inhibition, whereas observations of similar frontal theta activity would support the theory that frontal areas maintain goal-directed behaviour.

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In a previous study we reported increased frontal synchronization within the theta frequency range during correct and failed switches to an alternate response (Cheyne et al., 2012). We interpreted this frontal theta signal as reflecting top-down inhibition of the prepotent (“go”) motor response, and error processing, respectively. However when comparing with a similar purely response inhibition task, an earlier MEG study observed only error-related frontal theta increases following unsuccessful rapid response inhibition, and not following successful no-go responses (Mazaheri et al., 2009). Despite this observation, there is some evidence that theta oscillations have a role response inhibition. In contrast with Mazaheri et al., 2009, several studies have reported higher theta power in no-go trials over go trials, although this may be driven by differences in task parameters (Harmony et al., 2009; Harper et al., 2014; Kirmizi-Alsan et al., 2006; Nakata et al., 2013). Thus it remains unclear what is the role for frontal theta in inhibition of a predominant response, and further, what cortical signals may contribute to cognitive control over habitual responding (cf. Anzak et al., 2012; Cheyne et al., 2012; Isoda and Hikosaka, 2007, 2008; Jansma et al., 2001; Munakata et al., 2011).

The existence of several inhibitory mechanisms that may be engaged for different situations has been suggested (Boecker et al., 2013), including a distinction between global and selective inhibition, (De Jong et al., 1990, 1995). Decreased excitability was found in task-irrelevant muscles during standard but not selective stopping (Majid et al., 2012). Additional event-related potentials (ERPs) were measured over frontal and parietal regions when stopping in contrast to when changing a motor response in a stop-change task; however these electrophysiological differences were accompanied by behavioural differences in stop or stop-change reaction time (Kramer et al., 2011).

In contrast, there is recent evidence that frontal areas simply maintain and execute goal-directed actions, and are not specific to particular task demands (Band and van Boxtel, 1999; Collette et al., 2005; Criado and Boulinguez, 2013; Jasinska, 2013; Kenner et al., 2010; Miller and Cohen, 2001; Munakata et al., 2011). In other words, performance of an alternate response is thought to require the same inhibitory mechanisms as response inhibition alone. There is evidence from functional imaging to support this view, indicating no differences in structural activation or ERP recordings during inhibition and alternate response tasks (Boecker et al., 2011; Donkers and van Boxtel, 2004; Kenner et al., 2010; Rangel-Gomez et al., in press). Frontal theta oscillations in particular have been implicated as a mechanism for cognitive control (Cavanagh and Frank, 2014).

A second aspect of frontal control mechanisms in inhibitory control is the degree to which motor output becomes highly automated, particularly in repetitive motor tasks involving prepotent responses. In this case, one predicts that the role of frontal control mechanisms is diminished. A dual-process theory of cognitive control, for example, proposes that the ability to inhibit or switch between habitual responses and rare or unpredictable alternatives requires the intervention of a control (Type 2) process on an automatic (Type 1) response (Evans and Over, 1996; Stanovich and West, 2000). Such actions require rapid communication between sensory, cognitive, and motor systems of the brain, which are each associated with various signalling mechanisms and frequency profiles (Adam et al., 2012; Cheyne et al., 2012; Jansma et al., 2001; Sumner and Husain, 2008). Thus, more automated responses should be associated with different patterns of brain activity than those under cognitive control, with less involvement of those brain areas involved in Type 2 processing. This hypothesis was supported in our previous study (Cheyne et al., 2012) where frontal theta activity preceding correct responses was diminished for trials with reduced reaction time (response speeding) which is thought to indicate periods of automatic responding (Cheyne et al., 2006b). Therefore, reduced frontal activation between different cognitive response tasks could simply reflect differences in task difficulty and learning effects, and the degree to which each task can be performed under similar levels of attentional control, leading to greater or reduced degree of automaticity. This

makes it difficult to interpret observations of frontal activations during inhibitory control across tasks with different levels of difficulty or attentional control (such as stop-tasks and go/no-go tasks) or different individuals performing the same task.

The main objective of this study is to address the question of the role of frontal theta in response inhibition using both a purely response inhibition task compared with a selecting an alternative response within the same subjects. These tasks have similar structure, levels of difficulty, and attentional demands, and generate highly prepotent responses to frequent ‘go’ cues. One task was the sustained attention to response task (SART) (Robertson et al., 1997), a go/no-go task with low probability of no-go ‘target’ cues, and the other a variant of the SART, the response switching task (Cheyne et al., 2009a), or go/switch. These tasks differ only in whether the non-go (no-go or switch) “target” cue requires inhibition of an index finger movement (no-go) or inhibition plus responding with an alternate response finger (switch).

Evoked and oscillatory cortical activity was measured using magnetoencephalography (MEG). Frequency-specific source localization methods were used to identify cortical oscillations and their generators that reflect mechanisms either common to, or differential between, complete inhibition and inhibition plus selection of an alternative response. Frequency-specific neuronal oscillations are thought to reflect a mechanism for both short- and long-range communication within the brain, as reflected by higher and lower frequency bands, respectively (Buzsaki and Draguhn, 2004; Cavanagh and Frank, 2014; Cheyne, 2013). We also compared the effects of time-locking of brain responses to sensory cues and motor responses, in order to examine whether cue-locked activity on correct no-go trials was specific to processing the target cue rather than inhibition of the response. Given that both tasks generate a large number of errors because of the use of an infrequent target cue (20% occurrence), we were able to analyze brain responses to failed inhibition trials (failure to no-go or failure to switch, respectively). We compared behavioural and neurophysiological parameters including reaction time, error rates, visual responses (as indexed by occipital alpha power decreases), and movement preparation (as indexed by beta power decreases). We examined frontal theta band activity associated with inhibitory control of the prepotent “go” response, as well as during error processing. Given the similar structure, levels of difficulty, and attentional demands between go/no-go and go/switch tasks, we predicted equivalent frontal theta activity for both tasks. We additionally measured sensorimotor gamma activity during different response types, as this also been associated with motor processes and cognitive control (Gaetz et al., 2013; Lisman and Jensen, 2013).

Materials and methods

Subjects

Thirteen healthy right-handed adults (5 females, range 21–35 years) participated in this experiment. All subjects were recruited from the Toronto area and provided informed consent using protocols approved by the Hospital for Sick Children Research Ethics Board. Data from one male participant was excluded due to poor adherence to task instructions.

Go/no-go and go/switch tasks

A target stimulus (the digit “3”) was preceded and followed by all other digits from “1” to “9” (non-target stimuli), each with an equal probability, with an overall 20% probability of the occurrence of a target stimulus. Each digit was presented for a fixed duration of 400 ms, which was selected based on average reaction times, in order to avoid a visual response or even possible distraction induced by the changing display (from stimulus to mask) during responding. This was followed by presentation of a stimulus mask (“X” symbol) that remained on for a

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