Attention and the readiness for action

Katharine S. Baker[a], Jason B. Mattingley[a], Christopher D. Chambers[b], Ross Cunnington[a,*]

[a] The University of Queensland, School of Psychology and Queensland Brain Institute, QLD 4072, Australia
[b] School of Psychology, Cardiff University, Cardiff CF10 3AT, United Kingdom

ARTICLE INFO

ABSTRACT

The initiation of voluntary action is preceded by up to 2 s of preparatory neural activity, originating in premotor and supplementary motor regions of the brain. The function of this extended period of pre-movement activity is unclear. Although recent studies have suggested that pre-movement activity is influenced by attention to action, little is understood about the specific processes that are involved in this preparatory period prior to voluntary action. We recorded readiness potentials averaged from EEG activity as participants made voluntary self-paced finger movements. We manipulated the processing resources available for action preparation using concurrent perceptual load and cognitive working memory load tasks. Results showed that pre-movement activity was significantly reduced only under conditions of high working memory load, when resources for planning action were limited by the concurrent cognitive load task. In contrast, limiting attentional resources in the perceptual load task had no effect on pre-movement readiness activity. This suggests that movement preparatory processes involve mechanisms of cognitive control that are also required for working memory, and not more general engagement of selective attentional resources. We propose that the extended period of pre-movement neural activity preceding voluntary action reflects the engagement of cognitive control mechanisms for endogenously orienting attention in time, in readiness for the initiation of voluntary action.

© 2011 Elsevier Ltd. All rights reserved.

1. Introduction

Voluntary movements are planned and represented in the brain before they are initiated. Functional magnetic resonance imaging (fMRI) suggests a crucial role for the supplementary motor area (SMA) in the preparation for voluntary action, with activity in this region consistently shown to precede activity of the primary motor cortex prior to the initiation of movement (Ball et al., 1999; Cunnington, Windischberger, Deecke, & Moser, 2003; Cunnington, Windischberger, & Moser, 2005; Wildgruber, Erb, Klose, & Grodd, 1997), a finding that has been replicated by studies using positron emission tomography (PET) (MacKinnon et al., 1996) and magnetoencephalography (MEG) (Erdler et al., 2000). Electroencephalographic (EEG) studies of the slow, negative, scalp-recorded potential known as the Bereitschaftspotential, or readiness potential (Kornhuber & Deecke, 1965), suggest that this preparatory activity begins up to 2 s prior to voluntary action.

While this pre-movement neural activity is considered to represent movement-specific planning of factors such as movement direction (Cui & Deecke, 1999), body part (Boschert & Deecke, 1986; Kitamura, Shibasaki, & Kondo, 1993), force (Becker & Kristeva,

1980), and speed (Becker, Iwase, Jurgens, & Kornhuber, 1976), its precise function over such an extended time scale prior to movement is unclear. The earliest component of pre-movement activity of the readiness potential, beginning up to 2 s prior to movement, is characterized by a slowly increasing negativity, maximal over the vertex (Shibasaki & Hallett, 2006), and is thought to reflect activity predominantly in the SMA, pre-SMA, and anterior cingulate motor areas (Ball et al., 1999; Cunnington et al., 2005). Later stage movement-specific planning and execution is thought to be reflected in the late component of the readiness potential, beginning approximately 500 ms before movement and with maximal amplitude over the motor cortex contralateral to the moving limb (Deecke, Scheid, & Kornhuber, 1969).

The function of this very early pre-movement neural activity is not clear. When responding or reacting to external stimuli, complex movements can be performed with very little preparation time if necessary, thus obligatory motor planning processes alone cannot account for such an early and long period of cortical activity preceding movement. Non-motor processes such as motivation to move (McAdam & Seales, 1969), intentional involvement (Kornhuber & Deecke, 1965), awareness of movement (Keller & Heckhausen, 1990), spontaneity (Libet, Wright, & Gleason, 1982; McArdle, Mari, Pursley, Schulz, & Braun, 2009), and freedom of movement selection (Dirnberger, Fickel, Lindinger, Lang, & Jahanshahi, 1998; Praamstra, Stegeman, Horstink, Brunia, & Cools, 1995), have been implicated as factors involved in early pre-movement activity.

* Corresponding author at: The Queensland Brain Institute, QBI Building (#79), St. Lucia, QLD 4072, Australia. Tel.: +61 07 3346 6300; fax: +61 07 3346 6301.
E-mail address: r.cunnington@uq.edu.au (R. Cunnington).

Neuroimaging studies have shown movement-related brain activity to be strongly modulated by the level of attention and intention involved in the movement (Lau, Rogers, Haggard, & Passingham, 2004). Anterior cingulate, prefrontal and premotor areas, including the SMA, are more active when attending to a movement being performed than when performing it automatically (Jueptner et al., 1997; Passingham, 1996; Rowe, Friston, Frackowiak, & Passingham, 2002) or when attention is occupied by a distractor task (Johansen-Berg & Matthews, 2002). Lau et al. (2004) found that activity in the pre-SMA was greater when participants attended to their intention to move, rather than to the action itself. This suggests that increased attentional and intentional involvement engages the higher motor areas involved in pre-movement planning, and that activity in the SMA in particular may represent intentional or cognitive processes that are strongly influenced by attention.

Attention, however, is not a unitary process, and the precise processes that contribute to early pre-movement preparatory activity therefore remain unclear. In this study, we compared how the engagement of selective attentional resources in a perceptual task and the engagement of cognitive resources involved in working memory each influence early pre-movement activity prior to voluntary action. While most previous studies of attention to action relied on instructing participants to direct attention towards particular aspects of their movement, here we used a dual-task paradigm in which two competing tasks were performed simultaneously. This is a well-controlled method for manipulating and examining effects of limited-capacity resources on a given task (Fisk, Derrick, & Schneider, 1986; Wickens, 1984). By combining a voluntary movement task with a secondary task in which the relative difficulty or "load" was varied parametrically, we could limit the degree to which resources could be allocated or engaged in the preparation for voluntary action.

Additionally, by comparing the effects of perceptual and cognitive load tasks, we were able to elucidate the specific processes involved during the early period of movement preparation. Our perceptual load task involved the detection of pre-specified target letters amongst a rapid sequential stream of distractor letters, with load manipulated by increasing the visual similarity of target and distractor letters, thereby engaging limited-capacity selection processes. The cognitive load task was a version of the *n*-back task, in which participants were presented with a stream of letters and were required to match the current stimulus with the one presented up to two items ago, thereby placing substantial demands on working memory (Owen, McMillan, Laird, & Bullmore, 2005). In a broad sense, both perceptual and cognitive load tasks could be considered to load attention, in that both limit the degree to which participants can attend or allocate resources to the planning for action. However, perceptual and cognitive load tasks are also likely to draw on different neural resources, based on the theory that there exist specialized and separable attentional processing modules (Allport, 1980; Wickens, 1980).

Crucially, to ensure that the load manipulations engaged processing resources in both tasks, we conducted a behavioral validation study, independent of the readiness potential experiments. While performing either the perceptual or cognitive load task, we measured participants' response times to detect occasional brief dot stimuli presented unpredictably on the left or right of the screen. This type of probe task is typically used as an index of processing demands amongst multiple tasks (Posner & Boies, 1971). Speed and accuracy of responses to the dot probes provide a measure of the extent to which processing resources are loaded by the secondary tasks (Fisk et al., 1986), thus indicating the effectiveness of our load manipulations.

While previous studies of attention to action have generally used fMRI, by using EEG to examine readiness potentials preceding movement initiation we were better able to distinguish the time periods during movement planning that are most influenced by attention to action. In particular, we aimed to examine the effect of attentional load on the earliest component of pre-movement activity beginning up to 2 s prior to movement. It is this component that is thought to reflect activity predominantly in the SMA, pre-SMA, and anterior cingulate motor areas (Ball et al., 1999; Cunnington et al., 2005), and it is this early period of pre-movement activity that appears to be most affected by Parkinson's disease (Cunnington, Iansek, Johnson, & Bradshaw, 1997).

Therefore, by examining pre-movement activity in the readiness potential prior to voluntary finger movement as participants performed the different load tasks, we aimed to determine how the engagement of selective attentional resources (as indexed by the perceptual attention task), or cognitive resources (as indexed by the working memory task), influence the early processes that precede the initiation of voluntary movement. If the planning for action, and corresponding pre-movement neural activity, relies on the engagement of selective attentional or cognitive resources, we would expect readiness potential amplitudes to be reduced with increasing load in the perceptual or cognitive load tasks.

2. Materials and methods

2.1. Participants

Three independent groups of participants were recruited: two groups for the studies of perceptual and cognitive load on pre-movement neural activity in the readiness potential, and a further group for the behavioral validation study of the load tasks. All participants were right-handed and all had normal or corrected-to-normal vision. All studies were approved by the relevant local human research ethics committees.

Eighteen healthy volunteers (8 male, 10 female) aged between 21 and 29 years (mean: 23.7 ± 2.1) completed the perceptual load task during voluntary finger movements. Two participants were excluded from analysis due to reduced quality EEG signal. Twenty-five healthy volunteers (14 male, 11 female) completed the cognitive load task during voluntary finger movement. They were aged 18–35 years (mean: 22.36 ± 3.62). Four were excluded from analysis, owing to excessively noisy EEG data and a failure to produce observable readiness potentials in all conditions. In both tasks, noisy or low quality EEG datasets were defined as those containing fewer than 80 readiness potential epochs per condition that were free of eye, muscle, or signal drift artefacts.

Twenty-six healthy volunteers (11 male, 15 female), aged 18–29 years (mean: 22.75 ± 2.35) completed the behavioral validation task. Thirteen participants were assigned to the perceptual load task and thirteen performed the cognitive load task. One participant was excluded due to a recording error.

2.2. Tasks and design

2.2.1. Finger movement task

Participants executed simple, self-paced finger movements while their EEG was recorded to measure the neural activity associated with planning for voluntary action. The movement was a brief sequence of button presses on a response pad, with the index-middle-index fingers of the right hand pressing left-right-left buttons, respectively. Participants were instructed to repeat this movement sequence approximately once every 4–5 s throughout the experiment, but were asked explicitly not to count or otherwise try to judge the time elapsed between each movement.

While performing these movements, participants also completed either the perceptual load task or the cognitive load task, described below. Despite being performed concurrently, we ensured that responses required for the finger movement task and load tasks did not interfere with one another, by keeping the responses required for the load tasks relatively infrequent, allowing time in between them to measure voluntary movement preparation. The investigations of perceptual load and cognitive load on movement preparatory activity were run as two separate experiments, in different groups of participants, but the same finger movement task was used for each.

2.2.2. Perceptual load task

Participants were required to detect pre-specified target letters amongst a stream of distractor letters, presented in rapid serial visual presentation (RSVP) form. The letter stream comprised all letters of the alphabet, shown in upper case and randomly ordered, and was displayed on a CRT monitor using Presentation software (Neurobehavioral Systems, Albany, CA). All letters were presented in white, size 80 Arial font (height = 1.5° of visual angle), against a black background, with the exception of the letters V and W, which appeared in red. Perceptual load was manipulated across three conditions, but the physical characteristics of the stim-
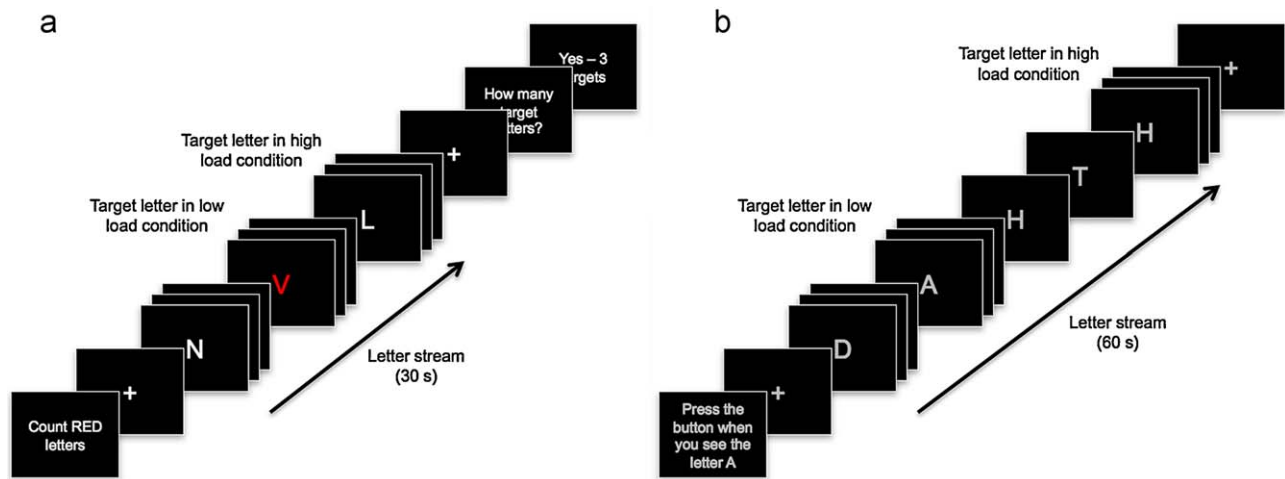
Fig. 1. Schematics showing the structure of a typical trial in the perceptual load task (a) and the cognitive load task (b). Examples of low- and high-load target letters are shown. Participants were required to respond to one category of target letter per block (low- or high-load), indicated by an instruction screen displayed at the beginning of each block. In no-load blocks, participants were required to fixate the letter stream but make no response. Perceptual load trials were 30 s long, with one letter presented every 150 ms. Cognitive load trials lasted 60 s with one letter presented every 800 ms. In the readiness potential experiments, participants completed each of the load conditions while simultaneously performing self-paced finger movements.

uli remained identical throughout, and only the instructions to participants were varied.

In the high-load condition, participants were asked to count the number of white T's and L's, appearing amongst a stream of predominantly white distractor letters. Since the targets in the high-load condition shared their features with most of the distractor items, this version of the task made significant demands on selective attention. In the low-load condition, participants counted the number of red letters appearing in each letter stream (V's and W's). As the red target letters could be distinguished from the white distractor letters by a unique feature (i.e., their color), they "popped out" of the sequential displays and thus made minimal demands on selective attention (in accordance with feature-integration theory (Treisman & Gelade, 1980). The no-load condition served as a baseline, in which participants were instructed simply to fixate the letter stream without responding to target items.

Each trial began with a white fixation cross, presented centrally for 3 s. This was followed by a 30 s letter stream during which stimuli were presented rapidly, one letter every 150 ms (Fig. 1a). Each letter stream contained between one and four of the relevant target letters. A second fixation cross then appeared to signal the end of the letter stream. Following each low- and high-load trial, the question "How many target letters?" was displayed, and participants indicated their answer by pressing the button corresponding to either 1, 2, 3, or 4 targets on their response pad. A feedback screen informed participants of whether or not their answer was correct, and displayed the actual number of target letters presented. In no-load trials, no response or feedback was required, and thus the next trial began immediately after the second fixation cross disappeared. The experiment was conducted in blocks of four trials, separated by brief rest periods. Each block began with an instruction screen indicating the category of target letters for that block. Participants initially performed two practice blocks of the high-load condition, followed by 27 experimental blocks (nine blocks for each of the no-, low- and high-load conditions), with the order of conditions counterbalanced across participants.

2.2.3. Cognitive load task

For the manipulation of cognitive load, we used an *n*-back working memory task. The mode of stimulus presentation was the same as in the perceptual load task, with the letter stimuli adjusted such that all were in pale grey lettering. Participants were required to respond to target letters across three cognitive load conditions, each placing a different level of demand on working memory. Once again, the physical stimuli remained identical across conditions.

In the high-load condition, participants were instructed to respond whenever they saw a letter that matched the one that had appeared in the previous-but-one display ("Press the button when you see a letter that matches the one you saw two letters back."). For the low-load condition, participants responded only to the appearance of one pre-specified letter ("Press the button when you see the letter A."). The no-load condition required participants to fixate the letter stream (as in the perceptual load task) without responding to the stimuli. Each trial began with a fixation cross, presented centrally for 5 s. This was followed by a 60 s stream during which one letter was presented every 800 ms, with each letter displayed for 200 ms (Fig. 1b). Each letter stream contained either two or three of the relevant target letters, to which participants indicated their responses by pressing a button on their response keypad with their right hand, next to but separate from the buttons used for voluntary finger movements. The experiment was conducted in blocks

of five trials, with short rest intervals between blocks. Each block was preceded by an instruction screen, informing participants of the category of target letters for that block. Participants initially completed one trial of each cognitive load condition as practice, followed by nine experimental blocks (three blocks for each of the no-, low- and high-load conditions), with the order of conditions counterbalanced across participants.

2.2.4. Behavioral validation study

The load tasks (perceptual and cognitive) as described above were each tested in conjunction with a dot-probe task in a dual-task paradigm, separate from the measurements of voluntary finger movement readiness potentials. Throughout each trial, white circles with a diameter of 0.02° of visual angle were briefly displayed (for 100 ms) either to the left or right of the letter stream at unpredictable intervals. The number of dot probes presented per trial was varied randomly, with 4–8 appearing during each 30 s perceptual load trial and 8–12 during each 60 s cognitive load trial. Participants responded to dot probes by pressing corresponding left or right response buttons as quickly as possible.

As there was no need to allow time for voluntary finger movements, fewer trials were included in this study compared to the readiness potential studies. The perceptual load task comprised four blocks of each of the high- and low-load conditions (plus two of each for practice) and two experimental blocks of the no-load condition. Blocks in the cognitive load task were shortened to include four trials each, and the study comprised one practice trial of each condition, followed by one experimental block of each condition.

2.3. Data acquisition

Participants were tested individually in a darkened room, to minimize distractions. They were seated in a comfortable chair approximately 1 m from the monitor on which letter stimuli were displayed. They positioned their fingers over the response pad and a pillow was placed under their right arm to help them remain still and comfortable and to reduce extraneous muscle movements. They were instructed to prioritize identifying target letters, and to consider the finger movements as a secondary task. They were asked to minimize blinking and other movements where possible. They then completed the practice trials before recording began.

Perceptual load EEG was recorded using Neuroscan Synamps 1 amplifiers, from 61 Ag/AgCl electrodes, positioned according to the extended International 10–20 system using an electrode Quick-cap (Compumedics Ltd., Melbourne, Australia). The data were sampled at a rate of 500 Hz and analyzed offline using Scan 4.3 software. Cognitive load EEG was recorded using an ActiveTwo BioSemi system with 64 Ag/AgCl electrodes (Neurospec, Bueren, Switzerland). Data were sampled at a rate of 1024 Hz and analyzed offline using BESA software (MEGIS Software, Grafelfing, Germany). For both tasks, electroocculogram (EOG) was measured using separate Ag/AgCl electrodes, positioned above and below the left eye for vertical EOG, and adjacent to the outer canthus of each eye for horizontal EOG.

2.4. Data analysis

The following EEG data processing procedures were implemented in all perceptual load and cognitive load datasets, over all conditions and electrodes. Raw data were referenced to linked mastoid electrodes. A spatial filter, based on the distri-

bution or topography of blink artefacts was created for each subject and used to correct blink artefacts from every channel. Lowpass and highpass filters of 30 Hz and 0.05 Hz, respectively, were applied to all data, although some datasets with very stable recordings were filtered using a 0.01 Hz highpass filter. Any filter chosen for a particular dataset was always applied equally across conditions. Epochs were then defined in relation to the first button-press in each movement sequence, spanning 2000 ms before the onset of movement to 500 ms afterward. Pre-movement epochs were created only in relation to the voluntary finger movements; any movements associated with the concurrent cognitive or perceptual load tasks (such as responses to target letters) were not considered voluntary and were not included in the analysis. Epochs were rejected if they overlapped with the presentation of (or response to) a target letter, other movement sequences, or the beginning or end of a trial, or if they contained artefacts caused by movement or poor signal. As the presentation of target stimuli within the letter streams was relatively infrequent, there was ample time between them to measure extended periods of pre-movement activity without contamination by target detection or responses. Cognitive load data were also corrected for excessive electrode drift, using a linear detrend procedure implemented in Matlab software (The Mathworks, Inc., Natick, MA). For datasets containing at least 80 artefact-free epochs per load condition, epochs were averaged to create event-related potentials. These were corrected to a baseline calculated as the mean amplitude from 2000 to 1500 ms before movement onset.

In order to quantify readiness potentials, mean amplitudes for each electrode of interest were taken across seven consecutive, non-overlapping time intervals of 200 ms each, beginning at −1400 ms through to 0 ms (the time of movement onset). Statistical comparisons of these mean amplitudes between conditions were conducted across a grid of nine fronto-central electrodes, including electrodes at midline (Fz, FCz, Cz), left lateral (F3, FC3, C3) and right lateral (F4, FC4, C4) locations. This grid encompassed the motor and premotor brain regions central to movement-related cortical activity. Electrode, time interval, and load condition were included as factors in three-way repeated measures ANOVAs, conducted separately on data obtained during perceptual and cognitive load tasks.

Behavioral measures of performance on the load tasks and the voluntary finger movement task were also analyzed. Accuracy of target letter detection was analyzed using t-tests, to verify that the pattern of difficulty across conditions was as intended. The interval between each successive self-paced finger movement sequence was taken as a behavioral index of movement uniformity, and was analyzed using repeated measures ANOVAs to ensure that the movement task was performed consistently across all conditions.

In the behavioral validation study, mean reaction time and accuracy of responses to dot-probe stimuli were also calculated for each load task. These were compared across conditions and tasks, using two-way mixed ANOVAs. An alpha level of .05 was used for all electrophysiological and behavioral statistics, and all post hoc tests were adjusted for multiple comparisons using a Bonferroni correction.

3. Results

3.1. Task performance

Performance on the load tasks, for both perceptual and cognitive load, are displayed in Fig. 2a. Target letter accuracy was found to be significantly higher in the low-load condition compared to the high-load condition, in both the perceptual load task, $t(15) = 6.89$, $p < .001$, and the cognitive load task, $t(20) = 13.86$, $p < .001$. This indicates that the pattern of relative difficulty between conditions was as expected, with the high-load condition being reliably more challenging.

Comparisons of inter-movement interval (Fig. 2b) revealed no significant differences across load conditions, either during the perceptual load task, $F(2, 30) = 2.07$, $p = .14$, or the cognitive load task, $F(2, 40) = 2.94$, $p = .064$, although the latter showed a trend towards longer intervals in the high-load condition.

3.2. Pre-movement neural activity: readiness potential

Readiness potentials observed at each electrode of interest during the perceptual and cognitive load tasks are shown in Fig. 3. Typical readiness potential morphology is evident in both tasks, with a slowly increasing negativity beginning approximately 1.5 s before the onset of movement across all load conditions, and maximum amplitude over central and left lateral electrode sites
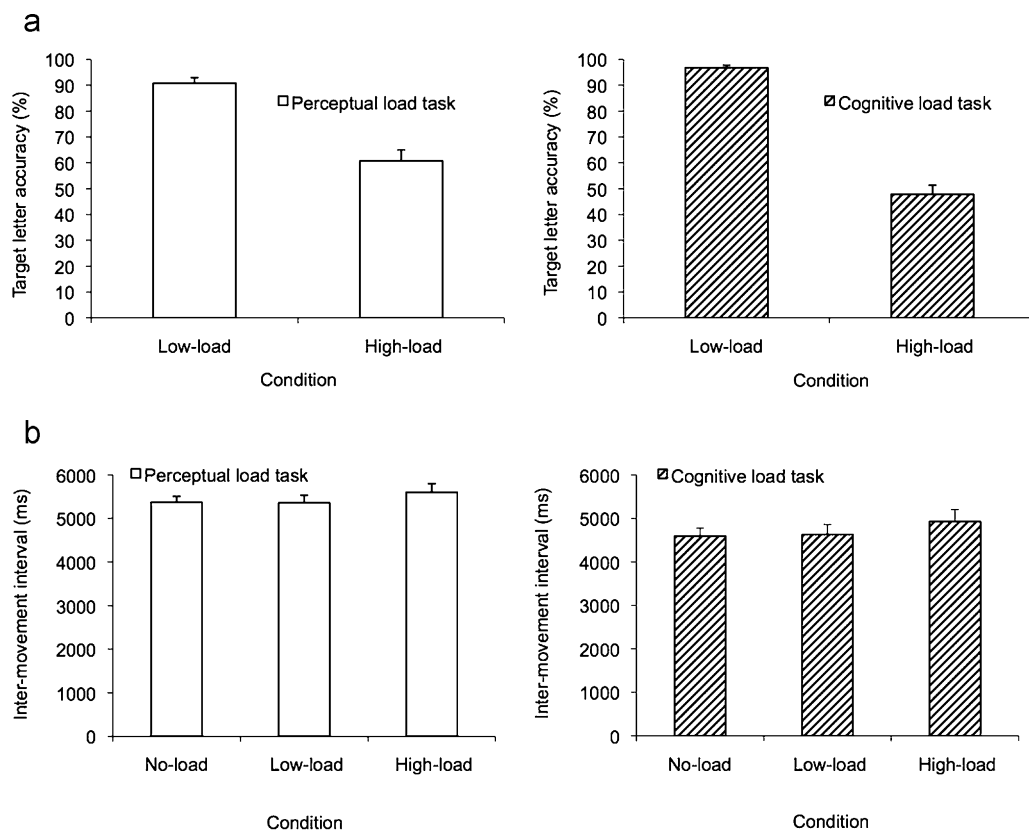

Fig. 2. Mean accuracy of target letter detection in the load tasks, for both perceptual and cognitive load (a), and mean interval between successive finger movement sequences performed during no-load, low-load, and high-load conditions of the perceptual and cognitive tasks (b). Error bars represent the standard error of the mean.
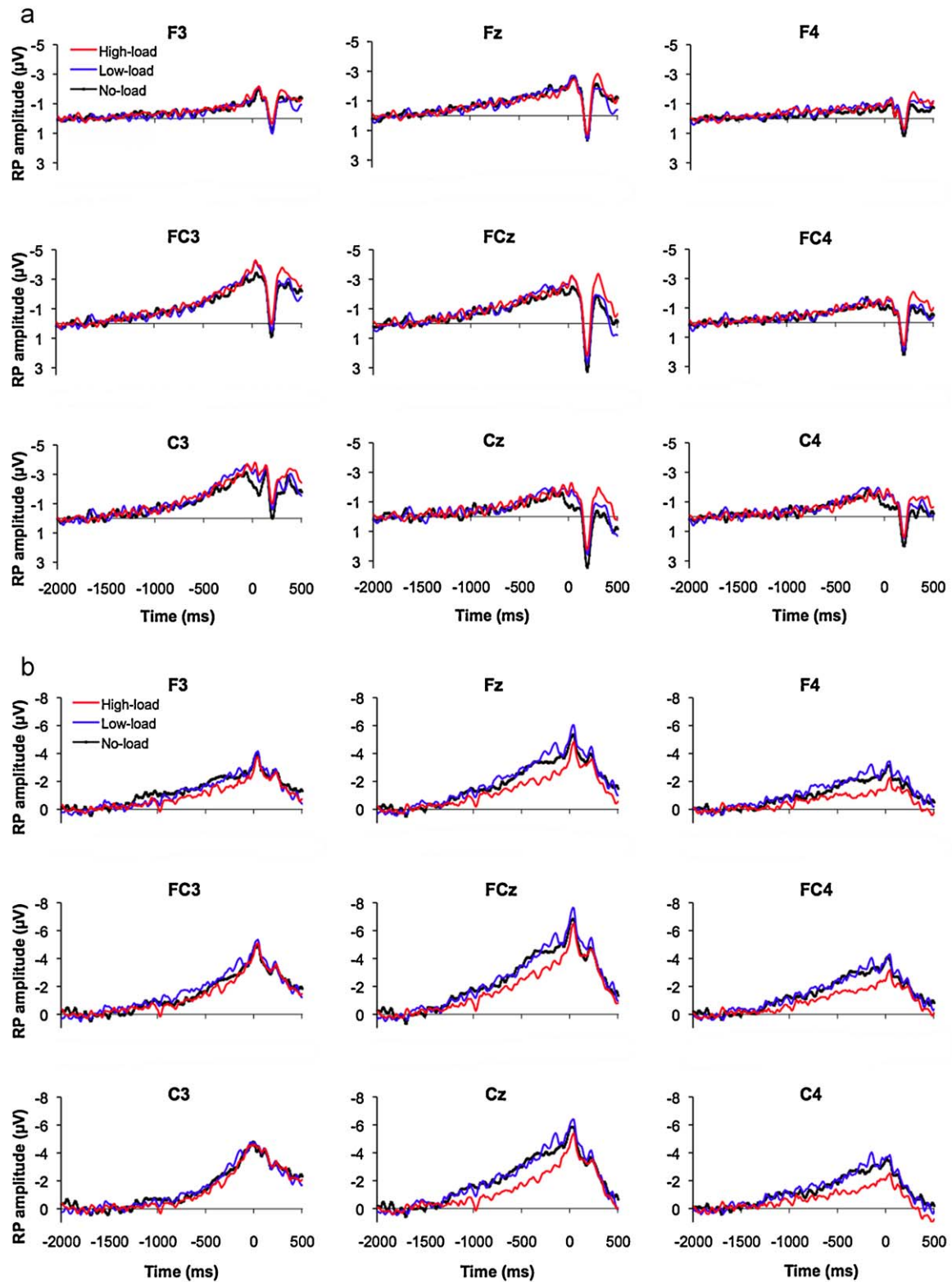
Fig. 3. Grand average readiness potentials shown at nine scalp electrode sites, in no-load, low-load, and high-load conditions, during both the perceptual load task (a) and the cognitive load task (b). A time interval from 2 s prior to movement onset to 0.5 s after movement onset is represented. Typical readiness potentials are observable during all conditions in both load tasks.

(i.e., predominantly contralateral to the moving hand). Potentials recorded during the perceptual load task displayed a positive peak following movement initiation that is not evident in the cognitive load data. Response buttons used in the perceptual task provided a stronger tactile "clicking" feedback when pressed, and we suggest that this larger positive component may be related to the extra sensory feedback from the button press. However this occurred well after the initiation of movement and therefore does not affect any of the measures of pre-movement activity in the readiness potential. Potentials recorded during the cognitive load task also displayed
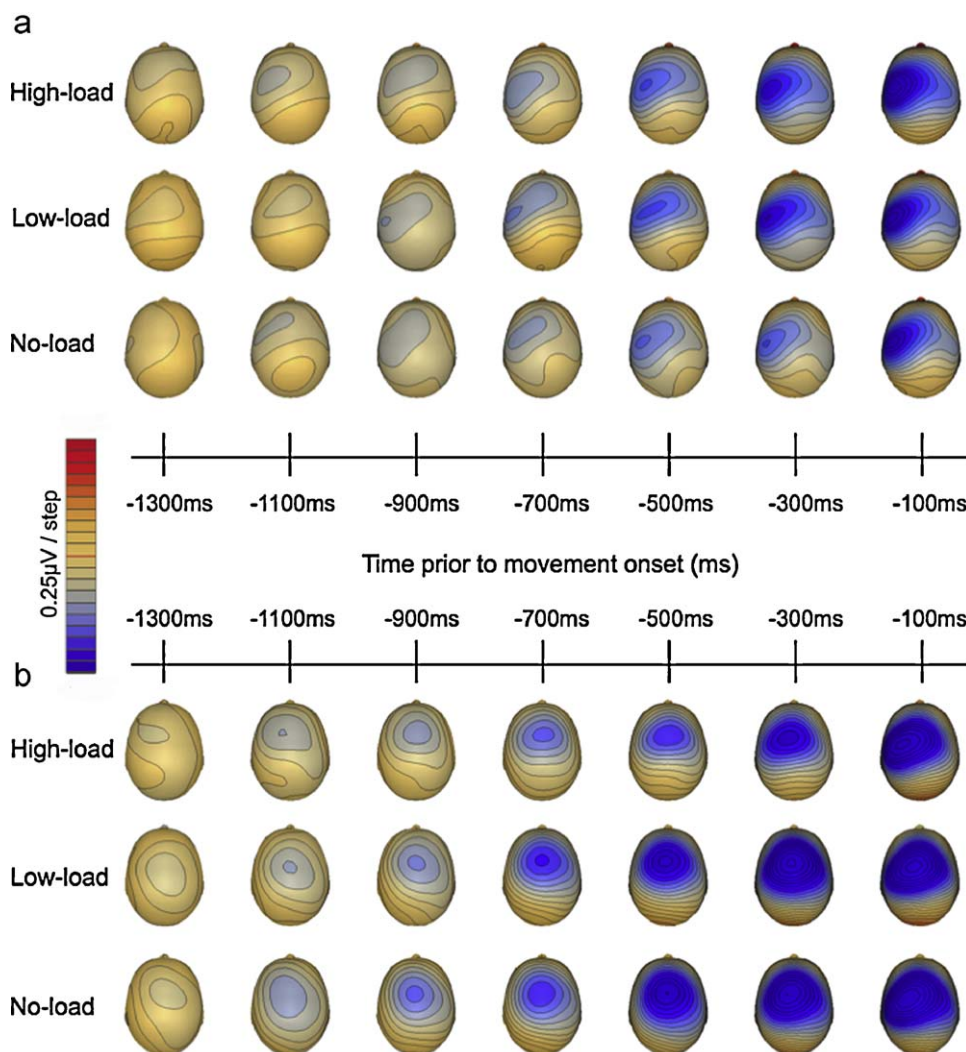
Fig. 4. Topographical maps representing neural activity at time points from 1300 to 100 ms before the initiation of movement, during each condition of the perceptual load task (a) and the cognitive load task (b). Negative activity (in blue) increased gradually over time with a left lateral shift just prior to movement onset.

higher amplitudes overall compared with those obtained during the perceptual load task, perhaps reflecting the use of different EEG recording systems in different participant groups. For our analysis of load effects, however, the critical comparisons were between the load conditions *within* each task, and these were properly controlled and manipulated within-subjects. Differences in absolute amplitudes between the two tasks are not important for our purposes, and should be interpreted with caution.

Topographical maps of pre-movement activity in each task (Fig. 4) show the expected pattern of activation, beginning over the vertex and becoming lateralized towards the left hemisphere over time. Accordingly, separate three-way repeated measures ANOVAs yielded significant main effects of time interval and electrode, and a significant time interval × electrode interaction, in both perceptual and cognitive load tasks ($p < .001$ for all comparisons). This showed that a characteristic readiness potential pattern, with increasing pre-movement activity over time maximal over central-midline electrodes, was produced across all conditions.

With regard to the load manipulation, during the perceptual load task, readiness potential traces (Fig. 3a) and mean amplitude data (Fig. 5a) showed little variation in amplitude across the three load conditions. Consistent with this, a three-way ANOVA revealed no significant main effects or interactions at any level involving the perceptual load variable ($p > .05$ for all comparisons). This indicates

that pre-movement neural activity in the readiness potential did not differ as a function of perceptual load.

In contrast, during the cognitive load task, the three-way ANOVA on mean amplitude data (Fig. 5b) revealed a significant load × time interval × electrode interaction, $F(96, 1920) = 1.54$, $p = .001$, suggesting that readiness potential amplitudes differed as a function of the cognitive load manipulation. Follow-up tests of simple effects (involving two-way and one-way ANOVAs) showed amplitude differences amongst load conditions at central and right lateral electrode sites. Of particular interest was whether these were modulated over time, such that differential effects in early and late readiness potential components could be observed.

Results of the ANOVAs led to two crucial findings. First, at the central-midline electrode Cz, effects of cognitive load began during the early readiness potential, more than 1 s prior to movement initiation. Specifically, across all time intervals from 1200 to 0 ms, there were significant main effects of load on readiness potential amplitude, $p < .05$ (except for the 800–600 ms time interval, for which $p = .057$). Post hoc pairwise comparisons between load conditions showed that each of these main effects was due to a reduction in readiness potential amplitude in the high-load condition compared with the no- and low-load conditions (high-load versus no-load comparisons significant at 1000–800 ms and 600–400 ms; high-load versus low-load significant at 600–400 ms and 400–200 ms).
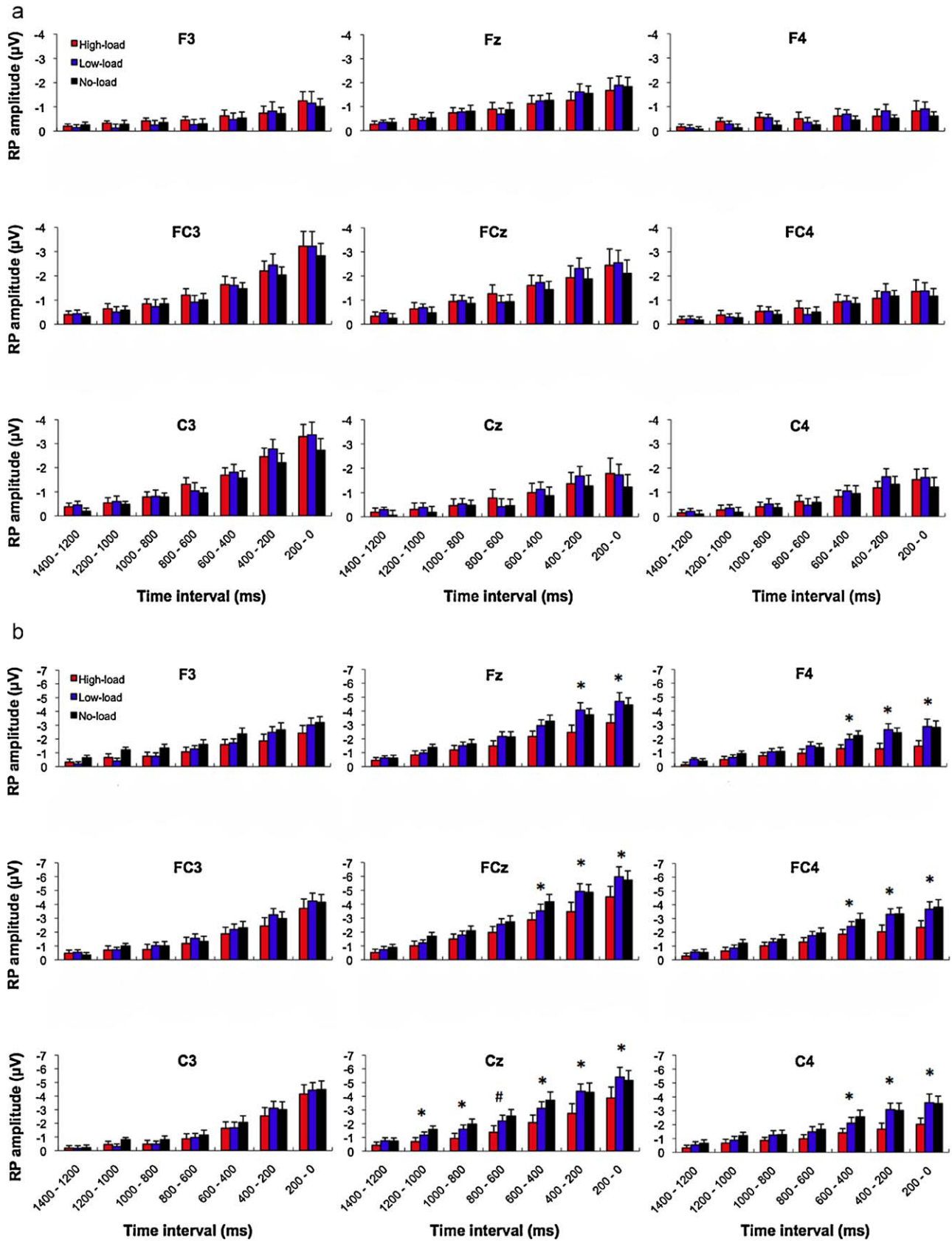
Fig. 5. Mean readiness potential amplitudes at nine electrode sites over seven consecutive time intervals (200 ms each), from 1.4 s prior to movement through to the onset of the first button press in the sequence, for readiness potentials recorded during each condition of the perceptual load task (a) and the cognitive load task (b). Error bars represent the standard error of the mean. Asterisks (*) represent the time intervals at which a significant main effect of cognitive load was found ($p < .05$), and the hash symbol (#) represents a main effect that approached significance ($p < .057$).
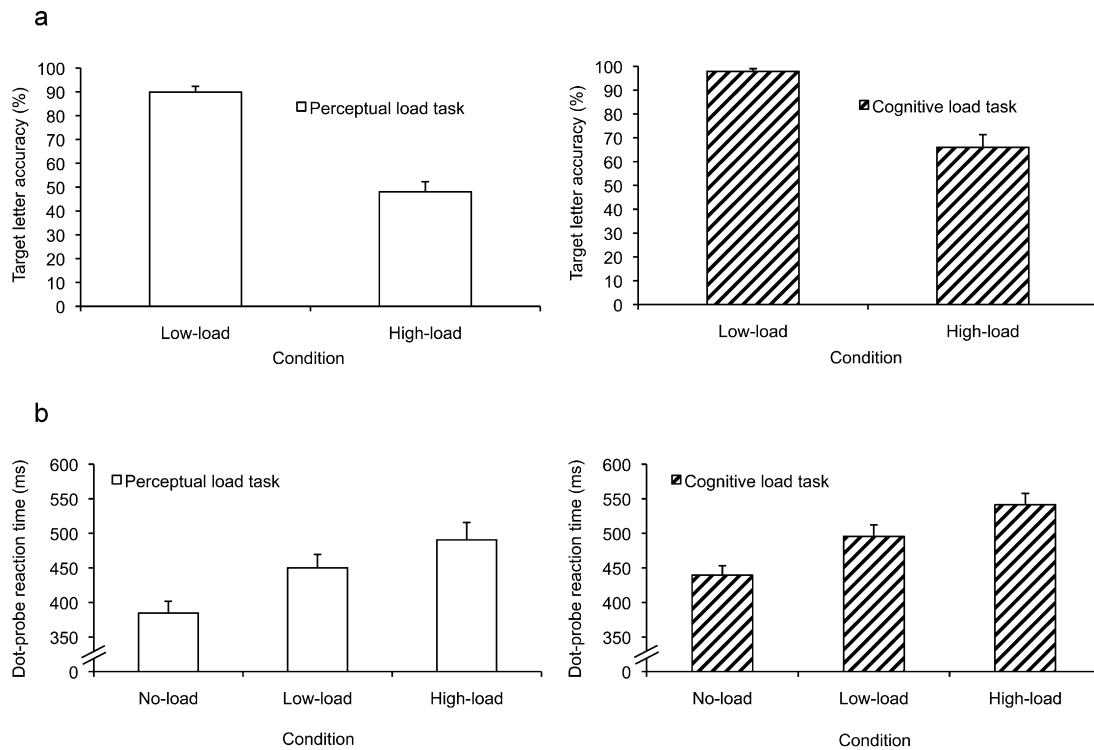
a

b

Fig. 6. Mean accuracy of target letter detection (a) and mean reaction times to dot-probe stimuli (b) during the behavioral validation of the perceptual load and cognitive load tasks. Error bars represent the standard error of the mean.

Second, over all other midline (Fz, FCz,) and right lateral (F4, FC4, C4) electrode sites, the cognitive load manipulation produced an effect over the late readiness potential. Significant main effects of cognitive load were found at every time interval from 600 ms through to movement onset, $p < .05$ (except for Fz, where the effect was not significant at 600–400 ms). Post hoc pairwise comparisons between load conditions again showed reductions in readiness potential amplitudes under conditions of high cognitive load, compared with low- and/or no-load conditions ($p < .05$ for all comparisons from 400 to 0 ms, and at 600–400 ms at electrode C4).

To further examine this effect of cognitive load on readiness potential amplitudes, and to ensure that effects were not simply due to differences in baseline activity, we performed a linear regression and compared the rate of increase in the readiness potential amplitude over the central-medial electrode Cz, from 1000 to 200 ms before movement. The readiness potential showed a shallower slope in the high-load condition compared with both the no-load condition, $t(20) = 2.53$, $p = .02$, and the low-load condition, $t(20) = 1.82$, $p = .08$, although the latter was a non-significant trend. This suggests that the load effects observed do not simply reflect higher sustained baseline activity under conditions of high working memory load, but reflect differences in the rate of increase in pre-movement activity.

Amplitude differences between no- and low-load conditions did not reach significance at any time interval or electrode site ($p > .05$ for all comparisons). There were also no significant effects of load over left lateral electrode sites.

3.3. Behavioral validation study

Participants' accuracy in detecting target letters during the dot-probe behavioral validation study is shown in Fig. 6a. Consistent with load task performance in the readiness potential studies, a two-way mixed ANOVA showed a significant main effect of load,

$F(1, 23) = 95.24$, $p < .001$, with follow-up comparisons showing significantly greater accuracy for low-load compared with high-load in both the perceptual load task and the cognitive load task ($p < .001$ for both comparisons). There was also a main effect of task, $F(1, 23) = 13.63$, $p = .001$, indicating that participants were overall more accurate on the cognitive load task (mean: 82%) than the perceptual load task (mean: 69%), but there was no significant load × task interaction, $F(1, 23) = 1.71$, $p = .204$.

Reaction times to the dot-probe stimuli (Fig. 6b) appear to lengthen as load increases, in both the perceptual load task and the cognitive load task. Accordingly, a two-way mixed ANOVA revealed a significant main effect of load, $F(2, 46) = 88.73$, $p < .001$. Follow-up comparisons of this load effect showed that, in both tasks, reaction times differed significantly amongst all conditions, such that they were shortest in the no-load condition, significantly longer in the low-load condition, and significantly longer again in the high-load condition ($p < .001$ for all comparisons). The main effect of task approached significance, $F(1, 23) = 4.16$, $p = .053$, with participants showing faster reaction times in the perceptual load task (mean: 442 ms) than in the cognitive load task (mean: 491 ms). Thus it appears that there is a difference in the response strategy employed by the participant group performing the perceptual task, who were faster at responding to dot probes in all conditions, and the group performing the cognitive task, who were more accurate at target detection. It was perhaps the faster rate of stimulus presentation in the perceptual task that prompted participants to prioritise speed of dot-probe responses at the cost of target detection accuracy. Crucially, though, there was no significant load × task interaction, $F(2, 46) = 0.19$, $p = .826$, indicating that the effect of increasing load on dot-probe reaction time performance was equal for perceptual and cognitive load tasks. The mean accuracy of responses to dot-probe stimuli was greater than 85% during both the perceptual load task and the cognitive load task, with no significant differences across load conditions ($p > .05$ for all tests).

4. Discussion

The aim of this study was to examine the effect of attention on the early pre-movement cortical activity associated with readiness for action, specifically examining the influence of perceptual and cognitive resources on readiness potential amplitudes. Overall, we found that pre-movement neural activity was not influenced by the availability of selective attentional resources in the perceptual load task, whereas it was significantly reduced when cognitive resources were limited under conditions of high versus low working-memory load.

The finding that pre-movement neural activity in the readiness potential is attenuated when cognitive resources are not readily available for movement preparation (i.e., under conditions of high working memory load) extends on previous neuroimaging studies showing that actively attending to one's movements increases motor preparatory activity (e.g. Jueptner et al., 1997; Passingham, 1996; Rowe et al., 2002). Crucially, we now further show that early stage pre-movement activity is not influenced generally by selective attention, but rather reflects the engagement of specific cognitive processes that overlap with cognitive control and working memory.

It is important to note that, in the behavioral validation study, the cognitive and perceptual load tasks were both equally effective in loading processing resources across conditions. Dot-probe reaction times lengthened and target detection accuracy deteriorated as load increased, equally for both cognitive and perceptual load tasks. Although the dot-probe task did not allow us to precisely equate the level of demand of the two primary tasks, it did show that there was a difference in the load requirements of the conditions in both tasks. Most importantly, the perceptual load task was found to affect behavioral dot-probe performance, yet still did not have any influence on pre-movement readiness potentials. Therefore, the effect of cognitive load alone on readiness potential amplitudes cannot be attributed simply to differential efficacy of the two load manipulations. Also, because manual responses to target letters were required in the cognitive load task, we specifically excluded readiness potential epochs for voluntary finger movements made within 2 s following a target response and epochs containing missed targets, so that even partial motor response activation in relation to missed targets was not present in the averaged readiness potentials. Results showed no difference in readiness potential amplitudes in the cognitive low-load condition (in which online target responses were made) compared with the no-load condition (which required no target responses), suggesting that any motor preparation associated with the manual target responses did not influence the readiness potentials preceding voluntary finger movements.

The reduction in pre-movement neural activity with cognitive load was most apparent at the central-midline Cz electrode site, located close to the SMA (a primary generator source of pre-movement activity (Cunnington et al., 2003), and was present as early as 1200 ms prior to movement onset. This clearly represents an effect on the early component of the readiness potential, prior to the later lateralized motor component thought to begin around 600–400 ms before movement onset (Deecke, Grozinger, & Kornhuber, 1976; Jahanshahi & Hallett, 2003). This later lateralized component of the readiness potential was also reduced under conditions of high cognitive load over right lateral and midline frontal electrode sites. This appears somewhat counter-intuitive, given that the late component is observed maximally over the left motor cortex (contralateral to movement), but represents a shifting topography of the readiness potential under high cognitive load (Fig. 4b). With the reduction in early midline activity under high load, the readiness potential topography is more strongly left lateralized over later time intervals, hence the reduced amplitudes seen

over the right hemisphere in the high-load condition. Interestingly, the left-lateralized late motor component was not significantly different across conditions. We suggest that this reflects the necessary movement programming processes involving contralateral motor cortex that are not influenced by cognitive load. This is consistent with previous evidence suggesting that the late component is influenced only by movement-specific features (see Shibasaki & Hallett, 2006), which were kept constant in this study.

Overall, our findings suggest that the earliest components of planning for voluntary action, and corresponding pre-movement neural activity, are strongly influenced by cognitive control processes that share resources with working memory. Based on previous neuroimaging studies, and our own recent work, we propose that it is particularly movement timing processes – deciding when to move, or cognitive control involved in endogenously orienting attention in time ready for action – that modulate the early neural activity prior to voluntary action. Previous fMRI studies have provided clear evidence for an overlap of neural resources recruited for executive functions in both working memory (as in our cognitive load task) and movement-related timing. The dorsolateral prefrontal cortex (DLPFC) is consistently activated during working memory tasks (Curtis & D'Esposito, 2003; Mayer et al., 2007; Rowe, Toni, Josephs, Frackowiak, & Passingham, 2000), including the *n*-back working memory task in particular (D'Esposito, Ballard, Aguirre, & Zarahn, 1998; Owen et al., 2005; Rodriguez-Jimenez et al., 2009). In the context of self-initiated movement, making a decision on when to move is a distinct and central component of intentional action (Brass & Haggard, 2008). The DLPFC is strongly implicated in the processing of such decisions, with increased activation seen when participants must select the timing for movement initiation (Jahanshahi et al., 1995; Jenkins, Jahanshahi, Jueptner, Passingham, & Brooks, 2000). The DLPFC is also important to the cognitive control of time estimation (Lewis & Miall, 2003), with the temporal processing of intervals of several seconds (such as the inter-movement intervals in the current study) thought to be cognitively mediated (Rammsayer, 1999). Therefore, cognitively controlled working memory and movement timing processes, including decisions on when to initiate movement, share neural resources in the prefrontal cortex.

Prefrontal regions important for cognitive control are strongly interconnected with medial frontal regions that are the primary source of early pre-movement activity (e.g. Aron, Behrens, Smith, Frank, & Poldrack, 2007; Wiese et al., 2004). These regions are thought to form a higher order motor network whereby the medial-frontal cortex, including the pre-SMA and anterior cingulate, provides an avenue for cognitive processes to influence the motor system (Hadland, Rushworth, Passingham, Jahanshahi, & Rothwell, 2001; Paus, 2001). Higher motor areas are also suggested to play a crucial role in timing (Nobre, 2001). For example, the premotor cortex and SMA are involved in orienting attention to points in time (Coull, Frith, Buchel, & Nobre, 2000; Coull & Nobre, 1998) and in selecting the right moment to initiate action (Deecke, Kornhuber, Lang, Lang, & Schreiber, 1985; Kornhuber, Deecke, Lang, Lang, & Kornhuber, 1989; Macar, Anton, Bonnet, & Vidal, 2004). In our own recent study (Bortoletto & Cunnington, 2010), we have shown that specifically attending to the timing of movement initiation, as well as involving greater activation of dorsal lateral prefrontal regions, also significantly enhances pre-movement neural activity in the early component of the readiness potential.

We therefore suggest that, when performing voluntary self-paced movements, participants focus on deciding the right moment to initiate their movements, relying on cognitive control mechanisms for selection and endogenously orienting attention in time. Imagine the high-board diver, standing, waiting, ready to initiate movement and jump from the platform. What cognitive and motor processes lead up to her deciding the moment to jump

and initiating her action? We suggest that the earliest component of pre-movement neural activity, evident in the readiness potential, represents cognitive rather than obligatory motor planning processes, perhaps representing the cognitive control processes needed for focusing or orienting attention in time to that crucial point of movement execution, readying the system for action.

Acknowledgments

References

Allport, D. A. (1980). Attention and performance. In G. Claxton (Ed.), *Cognitive psychology* (pp. 112–153). London: Routledge & Kegan Paul.

Aron, A. R., Behrens, T. E., Smith, S., Frank, M. J., & Poldrack, R. A. (2007). Triangulating a cognitive control network using diffusion-weighted magnetic resonance imaging (MRI) and functional MRI. *The Journal of Neuroscience*, 27(14), 3743–3752.

Ball, T., Schreiber, A., Feige, B., Wagner, M., Lucking, C. H., & Kristeva-Feige, R. (1999). The role of higher-order motor areas in voluntary movement as revealed by high-resolution EEG and fMRI. *NeuroImage*, 10(6), 682–694.

Becker, W., Iwase, K., Jurgens, R., & Kornhuber, H. H. (1976). Bereitschaftspotential preceding voluntary slow and rapid movements. In W. C. McCallum, & J. R. Knott (Eds.), *The Responsive Brain* (pp. 99–102). Bristol: Wright & Sons.

Becker, W., & Kristeva, R. (1980). Cerebral potentials prior to various force deployments. *Progress in Brain Research*, 54, 189–194.

Bortoletto, M., & Cunnington, R. (2010). Motor timing and motor sequencing contribute differently to the preparation for voluntary movement. *NeuroImage*, 49(4), 3338–3348.

Boschert, J., & Deecke, L. (1986). Cerebral potentials preceding voluntary toe, knee and hip movements and their vectors in human precentral gyrus. *Brain Research*, 376(1), 175–179.

Brass, M., & Haggard, P. (2008). The what, when, whether model of intentional action. *The Neuroscientist*, 14(4), 319–325.

Coull, J. T., Frith, C. D., Buchel, C., & Nobre, A. C. (2000). Orienting attention in time: Behavioral and neuroanatomical distinction between exogenous and endogenous shifts. *Neuropsychologia*, 38(6), 808–819.

Coull, J. T., & Nobre, A. C. (1998). Where and when to pay attention: The neural systems for directing attention to spatial locations and to time intervals as revealed by both PET and fMRI. *The Journal of Neuroscience*, 18(18), 7426–7435.

Cui, R.-Q., & Deecke, L. (1999). High resolution DC EEG of the Bereitschaftspotential preceding anatomically congruent versus spatially congruent bimanual finger movements. *Brain Topography*, 12(2), 117–127.

Cunnington, R., Iansek, R., Johnson, K. A., & Bradshaw, J. L. (1997). Movement-related potentials in Parkinson's disease. Motor imagery and movement preparation. *Brain*, 120(8), 1339–1353.

Cunnington, R., Windischberger, C., Deecke, L., & Moser, E. (2003). The preparation and readiness for voluntary movement: A high-field event-related fMRI study of the Bereitschafts-BOLD response. *NeuroImage*, 20(1), 404–412.

Cunnington, R., Windischberger, C., & Moser, E. (2005). Premovement activity of the pre-supplementary motor area and the readiness for action: Studies of time-resolved event-related functional MRI. *Human Movement Science*, 24(5–6), 644–656.

Curtis, C. E., & D'Esposito, M. (2003). Persistent activity in the prefrontal cortex during working memory. *Trends in Cognitive Sciences*, 7(9), 415–423.

D'Esposito, M., Ballard, D., Aguirre, G. K., & Zarahn, E. (1998). Human prefrontal cortex is not specific for working memory: A functional MRI study. *NeuroImage*, 8(3), 274–282.

Deecke, L., Grozinger, B., & Kornhuber, H. H. (1976). Voluntary finger movement in man: Cerebral potentials and theory. *Biological Cybernetics*, 23(2), 99–119.

Deecke, L., Kornhuber, H. H., Lang, W., Lang, M., & Schreiber, H. (1985). Timing function of the frontal cortex in sequential motor and learning tasks. *Human Neurobiology*, 4(3), 143–154.

Deecke, L., Scheid, P., & Kornhuber, H. H. (1969). Distribution of readiness potential, pre-motion positivity, and motor potential of the human cerebral cortex preceding voluntary finger movements. *Experimental Brain Research*, 7(2), 158–168.

Dirnberger, G., Fickel, U., Lindinger, G., Lang, W., & Jahanshahi, M. (1998). The mode of movement selection: Movement-related cortical potentials prior to freely selected and repetitive movements. *Experimental Brain Research*, 120(2), 263–272.

Erdler, M., Beisteiner, R., Mayer, D., Kaindl, T., Edward, V., Windischberger, C., et al. (2000). Supplementary motor area activation preceding voluntary movement is detectable with a whole-scalp magnetoencephalography system. *NeuroImage*, 11(6), 697–707.

Fisk, A. D., Derrick, W. L., & Schneider, W. (1986). A methodological assessment and evaluation of dual-task paradigms. *Current Psychology*, 5(4), 315–327.

Hadland, K. A., Rushworth, M. F. S., Passingham, R. E., Jahanshahi, M., & Rothwell, J. C. (2001). Interference with performance of a response selection task that has no working memory component: An rTMS comparison of the dorsolateral prefrontal and medial frontal cortex. *Journal of Cognitive Neuroscience*, 13(8), 1097–1108.

Jahanshahi, M., & Hallett, M. (2003). The Bereitschaftspotential: What does it measure and where does it come from? In M. Jahanshahi, & M. Hallett (Eds.), *The Bereitschaftspotential: Movement-related cortical potentials* (pp. 1–18). New York: Kluwer Academic/Plenum Publishers.

Jahanshahi, M., Jenkins, I. H., Brown, R. G., Marsden, C. D., Passingham, R. E., & Brooks, D. J. (1995). Self-initiated versus externally triggered movements: I. An investigation using measurement of regional cerebral blood flow with PET and movement-related potentials in normal and Parkinson's disease subjects. *Brain*, 118(4), 913–933.

Jenkins, I. H., Jahanshahi, M., Jueptner, M., Passingham, R. E., & Brooks, D. J. (2000). Self-initiated versus externally triggered movements: II. The effect of movement predictability on regional cerebral blood flow. *Brain*, 123(65), 1216–1228.

Johansen-Berg, H., & Matthews, P. M. (2002). Attention to movement modulates activity in sensori-motor areas, including primary motor cortex. *Experimental Brain Research*, 142(1), 13–24.

Jueptner, M., Stephan, K. M., Frith, C. D., Brooks, D. J., Frackowiak, R. S. J., & Passingham, R. E. (1997). Anatomy of motor learning. I. Frontal cortex and attention to action. *The Journal of Neurophysiology*, 77(3), 1313–1324.

Keller, I., & Heckhausen, H. (1990). Readiness potentials preceding spontaneous motor acts: Voluntary vs. involuntary control. *Electroencephalography and Clinical Neurophysiology*, 76(4), 351–361.

Kitamura, J., Shibasaki, H., & Kondo, T. (1993). A cortical slow potential is larger before an isolated movement of a single finger than simultaneous movement of two fingers. *Electroencephalography and Clinical Neurophysiology*, 86(4), 252–258.

Kornhuber, H. H., & Deecke, L. (1965). Hirnpotentialanderungen bei Willkurbewegungen und passiven Bewegungen den Menschen: Bereitschaftspotential und reafferente Potentiale. *Pflugers Archiv fur die gesamte Physiologie des Menschen und der Tiere*, 284(1), 1–17.

Kornhuber, H. H., Deecke, L., Lang, W., Lang, M., & Kornhuber, A. (1989). Will, volitional action, attention and cerebral potentials in man: Bereitschaftspotential, performance-related potentials, directed attention potential, EEG spectrum changes. In W. A. Hershberger (Ed.), *Volitional action* (pp. 107–168). Amsterdam: Elsevier.

Lau, H. C., Rogers, R. D., Haggard, P., & Passingham, R. E. (2004). Attention to intention. *Science*, 303(5661), 1208–1210.

Lewis, P. A., & Miall, R. C. (2003). Distinct systems for automatic and cognitively controlled time measurement: Evidence from neuroimaging. *Current Opinion in Neurobiology*, 13(2), 250–255.

Libet, B., Wright, E. W., & Gleason, C. A. (1982). Readiness-potentials preceding unrestricted 'spontaneous' vs. pre-planned voluntary acts. *Electroencephalography and Clinical Neurophysiology*, 54(3), 322–335.

Macar, F., Anton, J.-L., Bonnet, M., & Vidal, F. (2004). Timing functions of the supplementary motor area: An event-related fMRI study. *Cognitive Brain Research*, 21(2), 206–215.

MacKinnon, C. D., Kapur, S., Hussey, D., Verrier, M. C., Houle, S., & Tatton, W. G. (1996). Contributions of the mesial frontal cortex to the premovement potentials associated with intermittent hand movements in humans. *Human Brain Mapping*, 4(1), 1–22.

Mayer, J. S., Bittner, R. A., Nikolic, D., Bledowski, C., Goebel, R., & Linden, D. E. (2007). Common neural substrates for visual working memory and attention. *NeuroImage*, 36(2), 441–453.

McAdam, D. W., & Seales, D. M. (1969). Bereitschaftspotential enhancement with increased level of motivation. *Electroencephalography and Clinical Neurophysiology*, 27(1), 73–75.

McArdle, J. J, Mari, Z., Pursley, R. H., Schulz, G. M., & Braun, A. R. (2009). Electrophysiological evidence of functional integration between the language and motor systems in the brain: A study of the speech Bereitschaftspotential. *Clinical Neurophysiology*, 120(2), 275–284.

Nobre, A. C. (2001). Orienting attention to instants in time. *Neuropsychologia*, 39(2), 1317–1328.

Owen, A. M., McMillan, K. M., Laird, A. R., & Bullmore, E. (2005). N-back working memory paradigm: A meta-analysis of normative functional neuroimaging studies. *Human Brain Mapping*, 25(1), 46–59.

Passingham, R. E. (1996). Attention to action. *Philosophical Transactions of the Royal Society of London – Series B: Biological Sciences*, 351(1346), 1473–1479.

Paus, T. (2001). Primate anterior cingulate cortex: Where motor control, drive and cognition interface. *Nature Reviews Neuroscience*, 2(6), 417–424.

Posner, M. I., & Boies, S. J. (1971). Components of attention. *Psychological Review*, 78(5), 391–408.

Praamstra, P., Stegeman, D. F., Horstink, M. W. I. M., Brunia, C. H. M., & Cools, A. R. (1995). Movement-related potentials preceding voluntary movement are modulated by the mode of movement selection. *Experimental Brain Research*, 103(3), 429–439.

Rammsayer, T. H. (1999). Neuropharmacological evidence for different timing mechanisms in humans. *Quarterly Journal of Experimental Psychology Section B*, 52(3), 273–286.

Rodriguez-Jimenez, R., Avila, C., Garcia-Navarro, C., Bagney, A., de Aragon, A. M., Ventura-Campos, N., et al. (2009). Differential dorsolateral prefrontal cortex activation during a verbal *n*-back task according to sensory modality. *Behavioural Brain Research*, 205(1), 299–302.

Rowe, J. B., Friston, K., Frackowiak, R. S. J., & Passingham, R. E. (2002). Attention to action: Specific modulation of corticocortical interactions in humans. *NeuroImage*, 17(2), 988–998.

Rowe, J. B., Toni, I., Josephs, O., Frackowiak, R. S. J., & Passingham, R. E. (2000). The prefrontal cortex: Response selection or maintenance within working memory? *Science*, *288*(5471), 1656–1660.

Shibasaki, H., & Hallett, M. (2006). What is the Bereitschaftspotential? *Clinical Neurophysiology*, *117*(11), 2341–2356.

Treisman, A. M., & Gelade, G. (1980). A feature-integration theory of attention. *Cognitive Psychology*, *12*(1), 97–136.

Wickens, C. D. (1980). The structure of attentional resources. In R. Nickerson (Ed.), *Attention and performance VIII*. Hillsdale, NJ: Erlbaum.

Wickens, C. D. (1984). Processing resources in attention. In R. Parasuraman, & R. Davies (Eds.), *Varieties of attention* (pp. 63–101). New York: Academic Press.

Wiese, H., Stude, P., Nebel, K., Osenberg, D., Volzke, V., Ischebeck, W., et al. (2004). Impaired movement-related potentials in acute frontal traumatic brain injury. *Clinical Neurophysiology*, *115*(2), 289–298.

Wildgruber, D., Erb, M., Klose, U., & Grodd, W. (1997). Sequential activation of supplementary motor area and primary motor cortex during self-paced finger movement in human evaluated by functional MRI. *Neuroscience Letters*, *227*(3), 161–164.