NeuroImage 50 (2010) 1292–1302

Contents lists available at ScienceDirect

NeuroImage

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

The time course of activity in dorsolateral prefrontal cortex and anterior cingulate cortex during top-down attentional control

Rebecca Levin Silton [a,1], Wendy Heller [b,*], David N. Towers [a], Anna S. Engels [a,2], Jeffrey M. Spielberg [a], J. Christopher Edgar [b,3], Sarah M. Sass [a], Jennifer L. Stewart [a,4], Bradley P. Sutton [b], Marie T. Banich [c], Gregory A. Miller [d,*]

[a] Department of Psychology, University of Illinois at Urbana-Champaign, Urbana, IL, USA
[b] Department of Psychology and Beckman Institute Biomedical Imaging Center, University of Illinois at Urbana-Champaign, Urbana, IL, USA
[c] Institute of Cognitive Science, and Department of Psychology and Neuroscience, University of Colorado, Boulder, CO, USA
[d] Departments of Psychology and Psychiatry and Beckman Institute Biomedical Imaging Center, University of Illinois at Urbana-Champaign, Urbana, IL, USA

ARTICLE INFO

Article history:
Received 26 July 2009
Revised 25 November 2009
Accepted 15 December 2009
Available online 24 December 2009

ABSTRACT

A network of brain regions has been implicated in top-down attentional control, including left dorsolateral prefrontal cortex (LDLPFC) and dorsal anterior cingulate cortex (dACC). The present experiment evaluated predictions of the cascade-of-control model (Banich, 2009), which predicts that during attentionally-demanding tasks, LDLPFC imposes a top-down attentional set which precedes late-stage selection performed by dACC. Furthermore, the cascade-of-control model argues that dACC must increase its activity to compensate when top-down control by LDLPFC is poor. The present study tested these hypotheses using fMRI and dense-array ERP data collected from the same 80 participants in separate sessions. fMRI results guided ERP source modeling to characterize the time course of activity in LDLPFC and dACC. As predicted, dACC activity subsequent to LDLPFC activity distinguished congruent and incongruent conditions on the Stroop task. Furthermore, when LDLPFC activity was low, the level of dACC activity was related to performance outcome. These results demonstrate that dACC responds to attentional demand in a flexible manner that is dependent on the level of LDLPFC activity earlier in a trial. Overall, results were consistent with the temporal course of regional brain function proposed by the cascade-of-control model.

A network of brain regions supports top-down attentional control (Banich, 2009; Banich et al., 2000a,b, 2009; Buschman and Miller, 2007; Kerns et al., 2004; Liu et al., 2006; MacDonald et al., 2000; Miller and Cohen, 2001). A number of functional magnetic resonance imaging (fMRI) and positron-emission tomography (PET) studies have identified left dorsal lateral prefrontal cortex (LDLPFC) and dorsal anterior cingulate cortex (dACC) as key brain regions that initiate and monitor the need for top-down attentional control and adjust performance based on contextual demands (Banich et al., 2000b; Botvinick et al., 2004; Carter et al., 1999; Cohen et al., 2000; MacDonald et al., 2000; Milham et al., 2003a). Although these findings are robust, few studies have evaluated the time course of relevant activity in these brain regions during attentional control tasks, in part because fMRI and PET provide limited temporal resolution.

Research investigating the time course of attentional control in healthy controls has relied largely on scalp event-related brain potential (ERP) methods (Donkers and van Boxtel, 2004; Holroyd, 2004; Jackson et al., 1999; Kiefer et al., 1998; Liotti et al., 2000; West, 2003; West et al., 2004). Scalp ERP methods have temporal resolution on the order of milliseconds, but this temporal resolution often comes at the expense of spatial resolution. To date, no known study has integrated hemodynamic and electrocortical methods to identify the time course of regional brain activity associated with top-down attentional control. Such an approach has great potential to advance theories of attentional control. Identifying the temporal course of activity in brain regions implicated in attentional control is crucial to improving understanding of the individual roles of these brain regions as well as how they function in conjunction as a network and how they may go awry in mental illness.

fMRI and PET studies employing the color-word Stroop task (e.g., Stroop, 1935) have offered some insight into the role and time course of LDLPFC and dACC during top-down attentional control (Banich, 2009; Botvinick et al., 2004; Kerns et al., 2004). The "Stroop

* Corresponding authors. Department of Psychology, University of Illinois, Champaign, IL 61820, USA.
E-mail addresses: w-heller@illinois.edu (W. Heller), gamiller@illinois.edu (G.A. Miller).
[1] Current address: Department of Child and Adolescent Psychiatry and Behavioral Medicine, Seattle Children's Hospital, Seattle, WA, USA.
[2] Current address: Department of Psychology and Social, Life, and Engineering Sciences Imaging Center, Pennsylvania State University, Philadelphia, PA, USA.
[3] Current address: Department of Radiology, The Children's Hospital of Philadelphia, Philadelphia, PA, USA.
[4] Current address: Department of Psychology, University of Arizona, Tucson, AZ, USA.

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doi:10.1016/j.neuroimage.2009.12.061

interference effect" refers to a typical response pattern involving longer reaction time (RT) following incongruent stimuli (the word "red" in blue ink) than congruent (the word "red" in red ink) or neutral stimuli (a non-word such as "XXXX" or a non-color word, such as "bond," in red ink). MacDonald et al. (2000) examined brain activity for incongruent stimuli when the color had to be named, which requires an override of the more automatic process of word reading. They found more LDLPFC activity for color naming than for word reading. Banich et al. (2000a) found activation of bilateral DLPFC regions in both a standard color-word Stroop and a spatial-word Stroop task, indicating engagement of this region regardless of whether the task-relevant feature was an item's color or its spatial location. Furthermore, they found that this effect did not vary depending on the type of information to be ignored, as DLPFC was activated both for a color-word Stroop task and for a color-object Stroop task. Similarly, Fan et al. (2003) showed that LDLPFC was activated during both the Stroop task and the Spatial Conflict task (which involved nonverbal stimuli). Banich et al. (2000b) proposed that DLPFC provides a top-down attentional set toward task-relevant information and processes (e.g., ink-color identification). Although presumably such an attentional set would be imposed early on in the course of activity, this hypothesis has not been explicitly tested with data that can precisely address the temporal course of LDLPFC activity.

Beginning with the work of Pardo et al. (1990), much hemodynamic neuroimaging research has emphasized the role of ACC during Stroop performance (e.g., Botvinick et al., 2001, 2004; Casey et al., 2002; MacDonald et al., 2000; Mohanty et al., 2007). Pardo et al. (1990) found more ACC activity during incongruent than congruent trials. This result has been replicated using a comparison between incongruent and congruent conditions (Carter et al., 1995) as well as incongruent and neutral conditions (Bench et al., 1993). MacDonald et al. (2000) reported that participants who showed more Stroop interference tended to have more dACC activity and that dACC, but not LDLPFC, distinguished incongruent and congruent trials. These findings have encouraged theorizing about the role of the dACC during tasks that involve high levels of conflict that demand resolution (Botvinick et al., 2001, 2004). However, the precise roles of LDLPFC and dACC remain uncertain, in part due to the paucity of relevant time course information for regional brain activity.

The cascade-of-control (cascade) model proposes that DLPFC guides top-down attentional processing, and later dACC activity is thought to be involved in resolving response-related attentional processes (Banich, 2009; Liu et al., 2006; Milham et al., 2001, 2003a,b; Milham and Banich, 2005). Using a variant of the Stroop task, Milham et al. (2001) found that dACC was activated when the word identified an ink color that represented an alternative (conflicting) response, but not when the word identified an ink color that was not a possible response (the word conflicted with regard to semantics, but not with regard to a response). Further evidence for a dissociation between DLPFC and dACC was provided by Liu et al. (2006), who found that, unlike dACC activity, DLPFC activity was relatively impervious to whether a particular word was mapped to one or more responses. These findings are in accord with the view that, within a trial, DLPFC takes a dominant early role in top-down attentional control and that dACC is involved in later stages of selection that are linked to response-related processes (Liu et al., 2006).

ERP source analysis offers a promising method to evaluate the time course of DLPFC and dACC activity during the Stroop task. Scalp ERP color-word Stroop studies have been inconsistent, with an N400 component emerging most often (some color-word Stroop studies have referred to this component as the N450). N400 has been characterized as a distributed scalp ERP component (latency 400 ms to 500 ms) that is larger (more negative) during incongruent than during congruent trials (Hanslmayr et al., 2008; Holmes and Pizzagalli, 2008; Liotti et al., 2000; Markela-Lerenc et al., 2004). N400 is thought to reflect dACC activity and has been theorized to be related to processes occurring at the response stage (Hanslmayr et al., 2008; Holmes and Pizzagalli, 2008; Liotti et al., 2000; West et al., 2004). It remains unclear whether this component is the same as the classic N400 first identified by Kutas and Hillyard (1980).

An earlier component, N200, has sometimes been reported in the color-word Stroop (Holmes and Pizzagalli, 2008) and other visual interference tasks. This negative, frontally distributed component is thought to be generated by inferior/lateral PFC (Jackson et al., 1999; Kiefer et al., 1998) or dACC (van Veen and Carter, 2002, Yeung et al., 2004). N200 has also been associated with conflict monitoring (Donkers and van Boxtel, 2004; Holmes and Pizzagalli, 2008; Yeung et al., 2004). The exact process that is being indexed by this very early potential remains unclear.

Several recent studies have used ERP source analysis with Stroop data (Badzakova-Trajkov et al., 2009; Hanslymayr et al., 2008; Holmes and Pizzagalli, 2008; Liotti et al., 2000; Markela-Lerenc et al., 2004; West, 2003; West et al., 2004). Source analyses point to dACC activity occurring at 400–500 ms (Badzakova-Trajkov et al., 2009; Hanslmayr et al., 2008; Holmes and Pizzagalli, 2008; Liotti et al., 2000; Markela-Lerenc et al., 2004). Liotti et al. (2000) used coordinates from Pardo et al.'s (1990) PET study to position a dACC dipole, while allowing the orientation of the dipole to vary. This dipole accounted for 85% of the variance at the peak of the activity (410 ms). Similarly, Hanslmayr et al. (2008) reported peak activity around 400 ms for dACC.

Markela-Lerenc et al. (2004) conducted source analysis using a difference waveform (incongruent- minus congruent-trial waveforms) in an attempt to isolate the processes specifically associated with the interference effect. They fit a model that involved a left PFC dipole and an ACC dipole. Somewhat supporting the cascade model, left PFC was maximally active at 400 ms, and ACC was maximally active at 470 ms. However, visual inspection of their published dipole waveforms suggests that the two dipoles may be redundant and that their model is better fit with a single dipole. Badzakova-Trajkov et al. (2009) also used a difference source waveform comparison method, identifying a dACC peak at 425 ms for the incongruent–congruent difference waveform, which is consistent with the findings from the other Stroop source analysis studies. However, source analysis performed on difference waveforms is problematic, since the subtraction method involved in calculating this waveform will tend to distort the scalp topography, which could result in compromised dipole locations and time courses. Source analyses that were based on a difference waveform should therefore be interpreted cautiously. To avoid such problems, the present study did not use difference waveforms.

Despite variance in participant selection, experimental design, and source analysis strategies, the converging findings are encouraging and suggest a robust effect likely related to dACC activity that occurs between 400 and 500 ms. This is also consistent with scalp ERP findings. This later dACC activity is likely related to later aspects of response selection, rather than earlier aspects of conflict monitoring, which would be expected to occur possibly as early as 200 ms. Overall, the temporal pattern of data revealed in the ERP literature provides strong support for the plausibility of the cascade model, but a more definitive test is needed.

The present study sought to resolve the question of the relative timing and magnitude of LDLPFC and dACC activity associated with top-down attentional control processes in the course of a trial by using the power afforded by the parallel acquisition of fMRI and ERP data. These data were obtained in separate sessions for a large set of 80 carefully screened undergraduate students while they performed the attentionally-demanding Stroop task. The scalp ERP data were analyzed to a limited degree with the sole purpose of replicating previous findings in order to show that the scalp topography is consistent with previous studies prior to moving forward with source analysis.