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The activation of interactive attentional networks

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Attention can be conceptualized as comprising the functions of alerting, orienting, and executive control. Although the independence of these functions has been demonstrated, the neural mechanisms underlying their interactions remain unclear. Using the revised attention network test and functional magnetic resonance imaging, we examined cortical and subcortical activity related to these attentional functions and their interactions. Results showed that areas in the extended frontoparietal network (FPN), including dorsolateral prefrontal cortex, frontal eye fields (FEF), areas near and along the intraparietal sulcus, anterior cingulate and anterior insular cortices, basal ganglia, and thalamus were activated across multiple attentional functions. Specifically, the alerting function was associated with activation in the locus coeruleus (LC) in addition to regions in the FPN. The orienting functions were associated with activation in the superior colliculus (SC) and the FEF. The executive control function was mainly associated with activation of the FPN and cerebellum. The interaction effect of alerting by executive control was also associated with activation of the FPN, while the interaction effect of validity by executive control was mainly associated with the activation in the pulvinar. The current findings demonstrate that cortical and specific subcortical areas play a pivotal role in the implementation of attentional functions and underlie their dynamic interactions.

Introduction

Attention refers to the activity of a set of brain networks that influence the priority of information processing for access to conscious awareness (Mackie et al., 2013; Posner and Fan, 2008). It can be conceptualized in specific functional and anatomical terms, with three separable networks of alerting, orienting, and executive control (Petersen and Posner, 2012; Posner and Fan, 2008; Posner and Petersen, 1990). The alerting network is responsible to achieve and maintain phasic and tonic states of readiness in order to process non-specific impending inputs and is associated with activation in the thalamus and a set of frontal and parietal regions, such as dorsolateral prefrontal cortex (DLPFC), anterior cingulate cortex (ACC) and anterior insular cortex (AI), and areas near or along the intraparietal sulcus (thereafter referred to as IPS) (Fan et al., 2005; Kinomura et al., 1996; Perin et al., 2010), which are part of the extended frontoparietal network (FPN) (Fan, 2014). The orienting network shifts the focus of attention to specific inputs within or among different sensory modalities, and is associated with activation in the frontal eye fields (FEF) and IPS (Corbetta et al., 2002; Corbetta and Shulman, 1998; Fan et al., 2005; Thompson et al., 2005). The executive control network detects and resolves conflict between competing mental processes (Fan et al., 2002, 2009) and is associated with activation in the ACC (Botvinick et al., 2001; Bush et al., 2000; Fan et al., 2005; MacDonald et al., 2000; Matsumoto and Tanaka, 2004), and other areas of the FPN (Fan, 2014). The synergy of the three attentional functions is needed to achieve cognitive control (Mackie et al., 2013), however, the neural substrates underlying the interactions of the attentional networks remains to be clarified.

Although the three attentional networks have been shown to act independently (Fan et al., 2002) and to be associated with distinct neural substrates (Fan et al., 2005), evidence suggests that the attentional networks also interact to influence performance (Callejas et al., 2004; Fan et al., 2009; Wen et al., 2013). Alerting has been shown to interact with executive control, resulting in an increase of the conflict effect (Fan et al., 2009). Orienting enhances the efficiency of executive control (Callejas et al., 2004; Fan et al., 2009; Spagna et al., 2015), and alerting

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has been shown to influence the behavioral effects of orienting (Callejas et al., 2004; Fuentes and Campoy, 2008; Spagna et al., 2014). However, neuroimaging studies have not yet systematically investigated brain regions and networks that support the interactions of attentional functions.

Much of the neuroimaging literature has focused on the cortical activity associated with the attentional functions. However, animal and human studies have also shown substantial evidence that subcortical regions play a critical role in attention (e.g., Fan et al., 2005; Karnath et al., 2002; Petersen et al., 1987; Rafal and Posner, 1987; Shipp, 2004). Alerting is influenced by the cortical distribution of the noradrenergic (NAergic) system that arises from the locus coeruleus (LC) (Beane and Marrocco, 2004; Marrocco and Davidson, 1998; Moruzzi and Magoun, 1949), a nucleus located in the dorsorostral pons which receives strong descending afferents from prefrontal brain regions such as the ACC (Aston-Jones and Cohen, 2005b). The presentation of a warning signal is often accompanied by activity in the LC (Petersen and Posner, 2012; Posner and Petersen, 1990). Orienting is modulated by cholinergic systems arising in the basal forebrain (Marrocco and Davidson, 1998). Subcortical activity related to the orienting function has been shown in the superior colliculus (SC) in the midbrain, as well as pulvinar and reticular nucleus in the thalamus (Ignashchenkova et al., 2004; Lee and Keller, 2006; Petersen et al., 1987; Salzmann, 1995; Shipp, 2004). Executive control relies on regions associated with the dopaminergic system (Marrocco and Davidson, 1998). The ventral tegmental area (VTA) projects to ACC and lateral prefrontal cortex, areas of the executive control network (Botvinick et al., 2004; Kerns et al., 2004; Raz and Buhle, 2006). Although subcortical regions have been shown to play a critical role in attention, the activation of these areas in attentional networks and their interactions remains to be thoroughly examined.

In this study, we used the revised attention network test (ANT-R) (Fan et al., 2009, 2012) together with functional magnetic resonance imaging (fMRI) to examine the neural substrates underlying the attentional functions and the interactions among them. We focused on identifying the activation of subcortical structures associated with the attentional networks and their interactions. We predicted that there would be substantial involvement of cortical and subcortical regions, such as LC, SC, VTA, and thalamus in the attentional functions and their interactions.

Materials and methods

Participants

Twenty-four adult volunteers (11 females and 13 males; mean age = 26.3 years; range = 18–49 years) participated in this study. All participants were right-handed and had normal or corrected-to-normal vision with an average estimated intelligence quotient of 115 ± 17. The Institutional Review Board of Icahn School of Medicine at Mount Sinai approved the consent procedure, and written informed consent was obtained from each participant prior to the experimental procedures.

The revised attention network test

The ANT-R (Fan et al., 2009) was designed to magnify the interactions among the three attentional functions based upon the original task (Fan et al., 2002) by manipulating the validity of spatial cues in order to measure the orienting operations of disengaging and moving + engaging. The details of the ANT-R are illustrated in Fig. 1. A central fixation cross and two boxes subtending 4.69° of the visual angle to the left and right of fixation remain visible on the screen throughout the duration of the task. In each trial, depending on the condition, either a transient cue (brightening of the box) is presented for 100 ms (the cued conditions) or the screen remains unchanged (the no cue condition). Three types of cues were used: (1) no cue (no brightening prior to target onset); (2) double cue (brightening of both boxes); and (3) spatial cue (one box brightening prior to target onset). The difference between the double cue and no cue conditions is that the former provides temporal information about the impending target, while in the

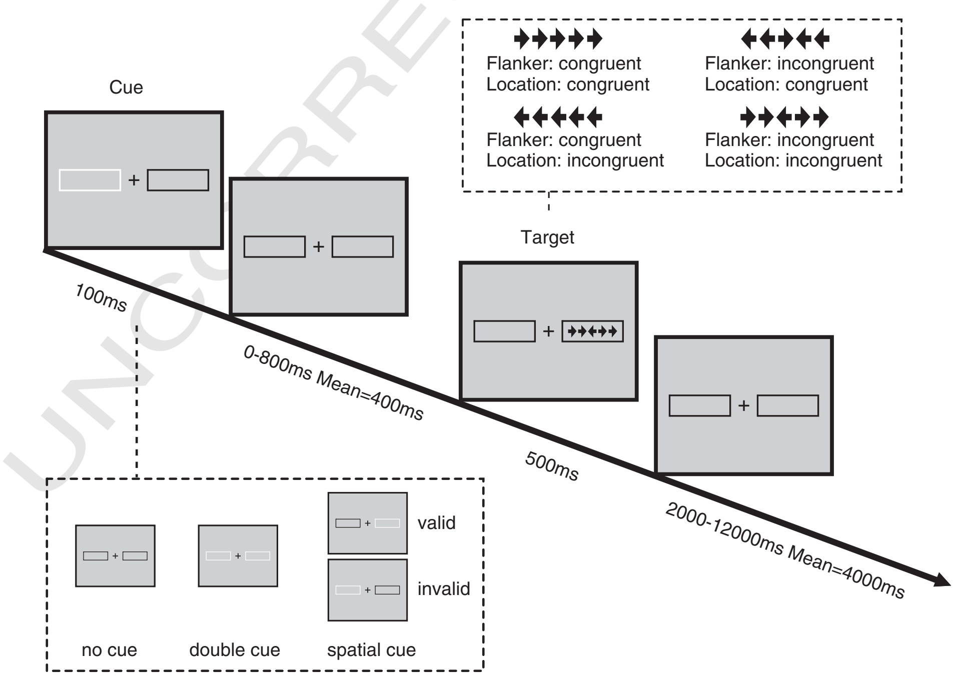

Fig. 1. Schematic of revised Attention Network Test (ANT-R). In each trial, depending on the cue condition (none, double, and valid or invalid cues), a cue box flashes for 100 ms. After a variable duration (0, 400, or 800 ms), the target (the center arrow) and two flanker arrows on both the left and right sides (congruent or incongruent) are presented for 500 ms. Participants must indicate the target's direction. Before the target appears, a cue in the form of a box flashing on one or both sides is displayed. The cue can be valid, which predicts the target position correctly, or invalid, which predicts the opposite position. There is also a double cue condition, in which both boxes flash, to provide temporal but not spatial information, while in the no cue condition no cue is presented. The post-target fixation period varies between 2000 and 12,000 ms. Note: The location congruency manipulation was not treated as a manipulation in data analysis in this study.

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