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Research report

Functional connectivity of parietal cortex during temporal selective attention

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ABSTRACT

Perception of natural experiences requires allocation of attention towards features, objects, and events that are moving and changing over time. This allocation of attention is controlled by large-scale brain networks that, when damaged, cause widespread cognitive deficits. In particular, damage to ventral parietal cortex (right lateralized TPJ, STS, supramarginal and angular gyri) is associated with failures to selectively attend to and isolate features embedded within rapidly changing visual sequences (Battelli, Pascual-Leone, & Cavanagh, 2007; Husain, Shapiro, Martin, & Kennard, 1997). In this study, we used fMRI to investigate the neural activity and functional connectivity of intact parietal cortex while typical subjects judged the relative onsets and offsets of rapidly flickering tokens (a phase discrimination task in which right parietal patients are impaired). We found two regions in parietal cortex correlated with task performance: a bilateral posterior TPJ (pTPJ) and an anterior right-lateralized TPJ (R aTPJ). Both regions were deactivated when subjects engaged in the task but showed different patterns of functional connectivity. The bilateral pTPJ was strongly connected to nodes within the default mode network (DMN) and the R aTPJ was connected to the attention network. Accurate phase discriminations were associated with increased functional correlations between sensory cortex (hMT+) and the bilateral pTPJ, whereas accuracy on a control task was associated with yoked activity in the hMT+ and the R aTPJ. We conclude that temporal selective attention is particularly sensitive for revealing information pathways between sensory and core cognitive control networks that, when damaged, can lead to nonspatial attention impairments in right parietal stroke patients.

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1. Introduction

Attention mechanisms serve to unify our experience of the world and enhance perceptual analysis of selected objects within the scene. Critically, attention mechanisms also promote our ability to disambiguate events that are rapidly changing over time. Because we live in a natural world that is in constant action, it is important to understand how temporal acuity of attention mechanisms plays a role in shaping visual awareness.

Psychophysical studies demonstrate that observers can parse temporal sequences into meaningful discrete units, but this ability is limited (for review, see Pöppel, 1997). For example, observers can detect very rapid space-time changes (up to 60 Hz, perceived as flicker or motion) encoded through low-level space-time filters in the visual system (Lu & Sperling, 2001). However, the ability to individuate component features of objects undergoing space-time changes can only be achieved at much slower speeds (7–10 Hz on average; Verstraten, Cavanagh, & Labianca, 2000). This sluggish acuity is comparable to estimates of the temporal limits of attentive selection as estimated by feature tracking (Aghdaee & Cavanagh, 2007; Cavanagh, 1992), is similar to the speeds at which the order of event components can be reported (ordinal features; Correa, Sanabria, Spence, Tudela, & Lupiáñez, 2006), and the speeds required to discriminate features within temporal patterns (phase discriminations; Battelli, Cavanagh, Intriligator, Tramo, & Barton, 2001).

In the brain, specialized networks exist that control spatial and feature-based selection of visual events, with extensive evidence that these control mechanisms shape the analysis of perceptual input (Kastner & Ungerleider, 2000). Allocation of attention to position and visual features is controlled by a large frontoparietal network subdivided into two major systems: a bilateral dorsal network (DAN) that controls spatial updating, attention-guided saccades, and the selection of important regions of space (Corbetta et al., 1998; Merriam, Genovese, & Colby, 2003); and a right lateralized ventral network (VAN) that controls nonspatial aspects of attentive selection, including reorienting the focus of attention to previously unattended features, filtering unattended items, and detection of behaviorally relevant events outside of the current focus of attention (Corbetta, Kincade, Lewis, Snyder, & Sapir, 2005; Gharabaghi, Fruhmann Berger, Tatagiba, & Karnath, 2006; Shulman et al., 2010; Stevens, Calhoun, & Kiehl, 2005). In particular, deactivation of the ventral attention network (VAN) is linked to sustained monitoring for task-relevant features and the active filtering of unwanted sensory input (Anticevic, Repovs, Shulman, & Barch, 2010; Shulman et al., 2003). This neural suppression is hypothesized to be controlled by signals from within the dorsal attention system or the default mode network (DMN; associated with control of introspective, or inward, cognitive processes; Corbetta, Patel, & Shulman, 2008; Fox, Corbetta, Snyder, Vincent, & Raichle, 2006).

The neural locus of control for temporal selection is not well understood. A handful of neuroimaging studies have identified bilateral regions in parietal cortex as more activated when subjects attend to timing over shape features, and when subjects are endogenously cued to the onsets of events (Coull & Nobre, 1998; Davis, Christie, & Rorden, 2009). In studies of patients with damage to parietal cortex, however, it is those individuals with damage in right parietal cortex, and not the left hemisphere, who often have difficulty with tasks that require the rapid parsing of temporal features. These include judging the temporal order of sequential items (Battelli, Pascual-Leone, & Cavanagh, 2007; Berberovic, Pisella, Morris, & Mattingley, 2004; Robertson, Mattingley, Rorden, & Driver, 1998), reporting the relative onset of two visual events (Decaix, Chokron, Bartolomeo, & Sieroff, 2001), and detecting simultaneity in features embedded within rapidly changing sequences (Battelli, Cavanagh, Martini, & Barton, 2003). Whereas hemispatial neglect manifests as a failure to attend and explore contralesional space, the temporal deficits in right parietal patients often linger after the severity of spatial neglect has resolved, can occur with no concurrent deficits in spatial attention, and are apparent across the entire visual field (including ipsilesional space; Husain et al., 1997; Battelli et al., 2003). Thus, timing tasks have proven to be especially sensitive in revealing subtle attention deficits not otherwise apparent from spatial orienting tasks. We hypothesize that these deficits may be due to the integrity of large scale brain networks connected to right parietal cortex that support nonspatial attention control.

The goal of this study is to examine how network connections in parietal cortex change in the context of a task that employs temporal selective attention. In these experiments, we analyzed the functional connectivity and neural activity in parietal cortex from neurologically intact individuals while engaged in a temporal selection task. Subjects viewed a four-token dynamic sequence and made simultaneous phase discriminations (attend the relative contrast of two tokens flickering in- or out-of phase) or static contrast discriminations. The phase discriminations required subjects to parse the dynamic sequence to extract the relative contrast of the tokens, whereas the stationary contrast judgment did not require temporal filtering. The phase discrimination task was selected because of its sensitivity in revealing full-field deficits in right parietal patients, with these patients requiring significantly slower flicker (approximately 2 Hz) to discriminate in-versus out-of-phase flicker (Battelli, et al., 2003). Right parietal patients have no impairments making contrast discriminations (personal communication, Battelli). Both tasks employed the same stimulus sequence with only the subjects' attention strategy changing between the conditions.

Successful phase discriminations were associated with deactivation in two regions of parietal cortex: bilateral posterior temporal parietal junction (pTPJ) and right lateralized anterior temporal parietal junction (R aTPJ). Functional connectivity analyses revealed the bilateral pTPJ to be strongly connected to the DMN and the R aTPJ to be connected to the VAN, both during fixation baseline and while engaged in task. Both regions added connectivity to the right hMT+ during both attention tasks, with connections between hMT+ and the bilateral pTPJ emerging on phase discrimination trials judged accurately. We found no evidence of visual feature-specificity or visual field preferences in either region of interest.

We conclude that temporal selective attention makes significant demands on core cognitive control networks, indicative of a possible "when" pathway of information flow that is