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Research report

Sustained activity within the default mode network during an implicit memory task

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ABSTRACT

Recent neuroimaging studies have shown that several brain regions – namely, the posterior cingulate cortex (PCC), ventral medial prefrontal cortex (vmPFC), and the bilateral angular gyrus – are more active during resting states than during cognitive tasks (i.e., default mode network). Although there is evidence showing that the default mode network is associated with unconscious state, it is unclear whether this network is associated with unconscious processing when normal human subjects perform tasks without awareness. We manipulated the level of conscious processing in normal subjects by asking them to perform an implicit and an explicit memory task, and analyzed signal changes in the default mode network for the stimuli versus baseline in both tasks. The functional magnetic resonance imaging (fMRI) analysis showed that the level of activation in regions within this network during the implicit task was not significantly different from that during the baseline, except in the left angular gyrus and the insula. There was strong deactivation for the explicit task when compared with the implicit task in the default mode regions, except in the left angular gyrus and the left middle temporal gyrus. These data suggest that the activity in the default network is sustained and less disrupted when an implicit memory task is performed, but is suspended when explicit retrieval is required. These results provide evidence that the default mode network is associated with unconscious processing when human subjects perform an implicit memory task.

1. Introduction

In recent years, converging neuroimaging studies have shown that several brain regions consistently exhibit hemodynamic signal decreases during many cognitive tasks when compared with passive states, such as the resting state with eyes closed, visual fixation, or passive viewing of simple stimuli (Shulman et al., 1997; Gusnard and Raichle, 2001; Mazoyer et al., 2001). These brain regions include the posterior cingulate cortex (PCC)/precuneus, ventral and dorsal medial prefrontal cortex (vmPFC, dmPFC), bilateral inferior parietal lobule (IPL, i.e., angular gyrus and supramarginal gyrus, Brodmann area – BA 39, 40), and middle temporal gyrus (MTG, BA 21, 22, 19). The deactivation in these brain regions varies little in their locations across a wide range of cognitive tasks (Shulman et al., 1997; Mazoyer et al., 2001). As the deactivation network is also

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thought to be more active during resting states, it is variably called the default mode network (Raichle et al., 2001), the conscious resting state (Binder et al., 1999; Mazoyer et al., 2001), or task-induced/independent deactivation (McKiernan et al., 2003).

One of the important issues is what functions this default mode network might subserve (Shulman et al., 1997; Gusnard and Raichle, 2001; Mazoyer et al., 2001; Raichle and Mintun, 2006). There are mainly three different approaches to investigate this issue. One is to find an abnormal population (e.g., coma or dementia) in which the default network is significantly different from normal subjects during resting states (e.g., Laureys et al., 1999; Lustig et al., 2003), and then infer that the default network is related to the functions that the abnormal population is impaired. The second is to find a task condition during which the activity in the default mode regions is sustained (e.g., Binder et al., 1999), or even increased (e.g., Gusnard et al., 2001), and then infer that the default network shares the similar cognitive process underlying the task. The third is to find relationship between the default mode regions and offline task performance (e.g., Wig et al., 2008), and then infer that the default network is related to the cognitive functions underlying the task.

Based on studies that adopted the approaches described above, the default mode network is regarded to be involved in different on-going information processing (Mazoyer et al., 2001; Raichle and Mintun, 2006), such as monitoring the internal mental and external environment, preparing for a potential threat (Gusnard and Raichle, 2001), representing self and body image (Gusnard and Raichle, 2001), and maintaining a coherent flow of mental activities. For example, Mason et al. (2007) found that mind-wandering is associated with activity in regions of the default network. In addition, individuals' reports of the tendency of their minds to wander are correlated with activity in this network. There are also remarkable overlaps between regions in the default network and brain regions involved in self-projection and social cognition (for reviews, see Buckner and Carroll, 2007; Schilbach et al., 2008). During the resting state, rather than being passively activated by sensory input, the default mode regions may continuously process information to remember the past (Christoff et al., 2004; Schilbach et al., 2008), to consider another person's perspective (Buckner and Carroll, 2007), to generate associations between object features (e.g., PCC and medial prefrontal cortex – mPFC. Bar and Aminoff, 2003; Bar, 2007), and to construct future plans (e.g., Hassabis et al., 2007). For example, the parietal cortex and the mPFC are involved in processing self-referential and socially relevant information (e.g., Lou et al., 2004; Mitchell et al., 2005; Buckner and Carroll, 2007). The autistic patients, who have deficits in emotion and social interactions, show less deactivation in the mPFC (Kennedy et al., 2006). These data thereby help to integrate different functions as forms of self-projection, and provide a social context in which events become personally meaningful (Buckner and Carroll, 2007; Schilbach et al., 2008).

Among these candidate functions, one interesting issue is to what extent these functions depend on conscious processing. Previous studies have suggested that the default mode network is associated with conscious awareness (e.g., Binder et al., 1999; Fiset et al., 1999; Laureys et al., 1999; Laureys, 2005). This hypothesis has gained support mainly from studies on abnormal conscious states. For example, activity in the medial/lateral parietal cortices and the PCC is reduced during situations when consciousness is absent, such as sleep, deep anesthesia, a vegetative state, propofol-induced loss of consciousness, and epileptic patients in general seizures (Fiset et al., 1999; Laureys et al., 1999; Blumenfeld et al., 2004; Laureys, 2005). On the other hand, activity in the default mode network is still detectable even during anesthesia and other unconscious states (Pinsk and Kastner, 2007; Seeley et al., 2007). For example, Vincent et al. (2007) have found that in anesthetized monkeys, the activity in PCC/precuneus is significantly correlated with the dorsal PFC and lateral temporoparietal cortex (i.e., area 7a and superior temporal gyrus), which is similar to the findings in humans.

As indicated by Tsuchiya and Adolphs (2007), consciousness can be divided by its state, or by its content. The consciousness state refers to the level of consciousness, such as wakefulness, sleep, or coma; whereas the consciousness content refers to what it is we are conscious of. During the conscious state, people can still unconsciously process many kinds of mental activities they are experiencing at that moment, although they may not be aware of what content they process (i.e., unconscious processing) (Christoff et al., 2004; Fransson, 2006). For example, people could unconsciously/automatically perceive the presented stimuli, encode them, and unconsciously retrieve them (Tulving & Schacter, 1990). People could also show preference or prejudice for other people, although they may not explicitly state the reason (Frith and Frith, 2008). There is evidence showing that the default mode network is associated with the unconscious state (e.g., Vincent et al., 2007), but it is unclear whether this network is associated with unconscious processing when normal human subjects perform tasks without awareness.

To address this issue, we manipulated levels of conscious processing in memory retrieval tasks (for reviews, see Tulving & Schacter, 1990; Schacter et al., 2004). After learning the word pairs during encoding, normal human subjects were asked to perform an implicit task (i.e., perceptual identification task) and an explicit task (associative recognition) during retrieval. The two tasks differ in whether subjects *retrieve* information with or without conscious processing. The implicit memory refers to the influence of prior experience on behavior in the absence of conscious awareness during retrieval, whereas explicit memory refers to the retrieval of information by conscious efforts (Schacter et al., 2004). As normal subjects are possible to consciously retrieve information during implicit memory tasks, it is critical to avoid this kind of possible explicit contamination in such studies (Henson, 2003; Schacter et al., 2004). Thus we controlled explicit memory performance at a chance level by using a perceptual encoding task during study, and subsequently by using a perceptual identification task during retrieval (Gabrieli et al., 1997; Yang et al., 2003), in which word pairs were quickly flashed with individually adjusted exposure durations. The behavioral dissociation between the implicit and explicit task was necessary to ensure that the unconscious manipulation was successful thus we could test the difference of baseline versus implicit/explicit task in the default mode regions.