NeuroImage 69 (2013) 120–125

Contents lists available at SciVerse ScienceDirect

NeuroImage

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

Escaping the here and now: Evidence for a role of the default mode network in perceptually decoupled thought

Jonathan Smallwood [a,*], Christine Tipper [b], Kevin Brown [c], Benjamin Baird [b], Haakon Engen [a], Joseph R. Michaels [b], Scott Grafton [b], Jonathan W. Schooler [b]

[a] Department of Social Neuroscience, Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany
[b] Department of Psychological and Brain Sciences, University of California, Santa Barbara, USA
[c] Department of Physics, University of California, Santa Barbara, USA

ARTICLE INFO

Article history:
Accepted 8 December 2012
Available online 20 December 2012

Keywords:
Absent-minded lapses
Daydreaming
Default mode network
Medial prefrontal cortex
Posterior cingulate
Mind-wandering
Response time
Stimulus-independent thought

ABSTRACT

Cognition that is not based on perception can lead to at least two different outcomes. In some situations, cognition that is independent of perception can allow actions to be selected other than those prescribed by immediate perceptual input. In others, cognition can be independent of perception and unrelated to the current behavioral goal allowing thoughts to develop that are largely independent of the actions involved in an external task. The default mode network (DMN) has been implicated in both of these kinds of perceptually decoupled thought. The current experiment used functional magnetic resonance imaging to explore whether a common region of this network was co-activated by both of these states. Both the medial pre-frontal cortex and the posterior cingulate – two major hubs of the DMN – showed greater activity when (i) actions that did not depend upon immediate perceptual input were faster and (ii) when actions based on perceptual input were slower. Together these data suggest that the DMN is important in cognition that is independent from perceptual input regardless of whether such thoughts result in action, or, instead compete with the behavioral goals of the moment.

Introduction

One distinguishing feature of higher order cognition is that it allows the agent *freedom from immediacy* (Shadlen and Gold, 2004) whereby information processing is not limited to that which emerges as a direct response to stimulus input. At least in humans, this can arise in two different ways. Sometimes cognition supports *actions* that are not an automatic response to events in the immediate stimulus environment. For example, when stopping to pick up laundry while driving home, our behavior is not prescribed by the external stimulus: Unlike a red traffic light, stopping is not an act we should take every time we see the laundromat. At other times cognition can proceed largely unencumbered by both external stimuli and immediate behavioral goals. When we daydream about a vacation on the commute to work self-generated information forms the content of thought. Thus a second form of freedom from immediacy arises from states of 'pure' internal mentation which have no direct basis in the external environment (referred to as stimulus independent thought) (Antrobus et al., 1967). The current experiment explored if similar neural processes underpin these two different types of *freedom from immediacy*: (a) situations in which actions are selected that could not be made on the basis of immediate stimulus input and (b) situations when cognition is decoupled from perception and unrelated to current behavioral goals.

The default mode network (DMN, (Buckner et al., 2008) is a constellation of brain regions with two main hubs (Andrews-Hanna et al., 2010) — the anterior medial pre-frontal cortex (aMPFC, BA 10) and the posterior cingulate cortex/precuneus (pCC/Pre, BAs 7, 23, 31). The DMN is recruited when decisions regarding external stimuli are made using content from memory, for example, making inferences about mental states of others (Mitchell et al., 2006), imagining the future (Schacter et al., 2007, 2008, 2012), making autobiographical plans (Gerlach et al., 2011; Spreng et al., 2010), or, in the simplest case, retrieving a memory based on an associated cue (Huijbers et al., 2011). In these studies there is a relatively tight connection between DMN activity and behavior because the cognitive processes lead to relatively immediate task relevant actions (e.g. an external response in a cognitive experiment).

The DMN is also active during SITs that have no relation to any external task being performed (Andrews-Hanna, 2011) such as daydreaming, mind-wandering, or absent-minded errors (Christoff et al., 2009; Mason et al., 2007; McKiernan et al., 2003, 2006; Stawarczyk et al., 2011; Weissman et al., 2006). Although states of self-generated thought such as mind-wandering may lead to behavioral outcomes over longer time frames, or lead to errors in a task,

* Corresponding author.
E-mail address: smallwood@cbs.mpg.de (J. Smallwood).

1053-8119/$ – see front matter © 2012 Elsevier Inc. All rights reserved.
http://dx.doi.org/10.1016/j.neuroimage.2012.12.012

they rarely make a direct contribution to immediate and accurate external task relevant actions.

Operationalizing cognition that is independent of perception

The DMN therefore has been implicated in two forms of cognition that allow freedom from immediacy: it allows cognition to guide actions that go beyond those prescribed by an external stimulus and it is implicated in thoughts that have no bearing upon immediate perceptual input or current task goals. The current experiment used functional magnetic resonance imaging (fMRI) to examine whether specific regions of the DMN are engaged during thoughts that do not depend upon perceptual input regardless of whether they result in task-related action. To test whether specific regions of the DMN network supports a general process through which cognition gains independence from perception (known as perceptual decoupling) we asked participants to perform two tasks. In one, *working memory* (WM), a sequence of numeric stimuli was encoded and participants were intermittently probed regarding the parity of the prior stimulus. In a second, *choice reaction time* (CRT), sequences of digits were monitored at a relatively minimal level for the intermittent occurrence of non-colored target and participants made responses that indicated the parity of the colored target.

In this paradigm actions are always initiated in response to colored stimuli. An important feature of this design was that the colored stimuli required participants to switch from a passive viewing mode to one entailing active external behavior. Although both induced this switch, in the WM task participants had to generate the action based on information stored internally (i.e. Was the previous number odd or even?), while in the CRT task the same decision is made based on perceptual information that is available at the moment that the action takes place (i.e. Is the current number odd or even?). Thus, actions made in the WM task depend on cognition unrelated to immediate perceptual input to a greater extent than do those in the CRT task. In relative terms, therefore, correct responses to the colored numbers in the WM task reflect perceptually decoupled thought that results in a task-relevant action.

Thoughts that are not prescribed by perceptual input and that are unrelated to external tasks goals cannot be operationalized as directly as those that lead to action; instead this state must be inferred indirectly. One method to do this exploits the fact that perceptually independent thought that is unrelated to the current task can compromise performance in tasks that depend upon detailed external attention (e.g. Weissman et al., 2006). In the current experiment we operationalized poor performance as longer response times (RT) and performed a trial-by-trial analysis of the neural responses that preceded longer RT. A perceptual focus is needed both when encoding WM non-targets and when responding to CRT targets and so based on the logic of Weismann et al. on the occasions when actions based on perceptual input are inefficient (e.g. RT is relatively long), we inferred that task-unrelated perceptually decoupling was likely to have occurred.

Table 1
A summary of how the different conditions allow an examination of the common role of memory and perception in the guidance of behavior.

Task		Stimulus type	
		Non colored	Colored
Choice reaction time (CRT)	Example stimulus	6	7
	Motor response	No	Yes
	Event frequency	High	Low
	Task relevance	No	Yes
	Guidance of cognition	Memory	Perception
Working memory (WM)	Example stimulus	3	?
	Motor response	No	Yes
	Event Frequency	High	Low
	Task Relevance	Yes	Yes
	Guidance of Cognition	Perception	Memory

Summary of experimental aims

To test whether perceptually decoupled thought depends on similar processes regardless of whether it results in immediate action, we sought evidence of brain regions whose activity patterns were common to two situations: (a) relatively fast responses for actions that depend upon memory rather than perceptual input and (b) relatively slower responses for actions that depend on perceptual input rather than memory. Importantly, regions with activity patterns which showed a crossover interaction of this type would support a process that was independent of immediate perception and that was not a direct consequence of a task, the need to make an active response, or the frequency that an event occurred (see Table 1).

Methods

Participants

16 neurologically healthy right-handed individuals participated in the current experiment (8 females, age range = 18 to 21).

Tasks

Participants performed two runs of both the CRT and the WM task using a counterbalanced design. Runs of both tasks consisted of a series of 32 mini-blocks. Each mini-block began with a series of non-colored numbers and ended with the presentation of a colored stimulus. In each run, 128 non-colored stimuli were presented and the number in each mini block was randomized. Each run lasted 560 s and on average 17.5 s of non-colored numbers preceded each colored event. In the CRT task the mini-blocks ended with the presentation of a red numeral. In the WM task mini-blocks were terminated by the presentation of a target trial (a red '?'). In both tasks, participants made a right-hand manual response to the colored targets using a button box. A left button indicated a target stimulus was odd while a right button push indicated that it was even. Each stimulus was presented for 1–1.5 s and was followed by a fixation cross lasting 1–2.5 s. Prior to performing each task in the scanner, participants were given practice runs of each that lasted approximately one minute. Task order was counterbalanced. Stimulus presentation used MATLAB (Version 7.5, The Mathworks Inc., Natick, MA) and the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997; Kleiner et al., 2007).

fMRI data acquisition

fMRI data were collected on a phased array research dedicated Siemens Magnetom Trio Tim 3.0 T scanner with a standard 12 channel head coil. The entire scanning session consisted of six scans, including four task-related functional scans, a resting state functional scan, and a high-resolution 3D anatomical scan. Functional scans used a 2D gradient echo echo-planar imaging (EPI) pulse sequence sensitive to T2* BOLD contrast (64×64 matrix, 192×192 mm FOV, 37 interleaved AC-PC oriented transverse slices, 3 mm × 3 mm in-plane resolution, 3 mm slice thickness, 0.5 mm slice gap, 2000 ms TR, 30 ms TE, 90° flip angle). Task-related scans acquired 280 functional volumes. The high-resolution structural image was acquired using a flash 3D pulse sequence sensitive to T1 contrast (256×256 matrix, 220×220 mm FOV, 192 interleaved saggital slices, 0.9×0.9 mm in-plane resolution, 0.89 mm slice thickness, 0.01 mm