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.

© 2012 Elsevier Inc. All rights reserved.

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

slice gap, 15 ms TR, 4.20 ms TE, 20° flip angle). Each functional scanning run began with the acquisition of four dummy volumes used to achieve steady-state tissue magnetization, which were discarded. A transistor–transistor logic (TTL) pulse sent out by the scanner at the onset of each viable EPI volume triggered the stimulus presentation software, and synched the beginning of each trial to the onset of the next complete image volume. All images were reconstructed off-line according to standard Siemens protocols and stored in DICOM format.

fMRI image processing

All preprocessing and analysis were performed using SPM8 (Wellcome Trust Department of Imaging Neuroscience, University College London, UK). Functional scans were realigned to their mean volume using a seventh degree B-Spline interpolation. Each participant's structural scan was co-registered to the mean of his/her functional volumes using an automated rigid-body transformation algorithm. Normalization to MNI space was performed using Unified Segmentation (Ashburner and Friston, 2005) and the subsequent images were resampled into $3\times3\times3.5$ mm voxels. Finally, images were smoothed with a 5-mm FWHM kernel. This relatively low smoothing kernel was chosen to ensure maximum anatomical specificity of the subsequent results.

Statistical analysis was performed using the general linear model framework implemented in SPM8. A high-pass filter (128 s), and an autoregressive model [AR(1)] was applied to correct for low frequency drift and correct for autocorrelation. Additionally, movement parameters, as estimated during realignment, were added as regressors of no interest to remove residual motion-related variance.

Results

Behavioral performance

Participants were accurate on both the WM ($M=.96$ (SE = .01) and the CRT task ($M=.96$ (SE = .01) and this did not vary by condition, $F(1,16)=.03$, $p=.86$. Consistent with previous behavioral studies (e.g. Baird et al., 2012; Smallwood et al., in press) correct RT was significantly shorter when participants performed the WM ($M=685$ ms ($SE=5.2$)) than the CRT (M = 730 ms (SE = 5.2)), $F(1,16)=6.0$, $p<.05$. RT is shorter during WM blocks because participants must continually maintain attention on each digit, whereas in the CRT task participants need only attend when the colored target is presented. Presentation of the colored stimulus in CRT therefore requires its identity to be encoded before the decision can be made; hence RT is longer than in the WM task.

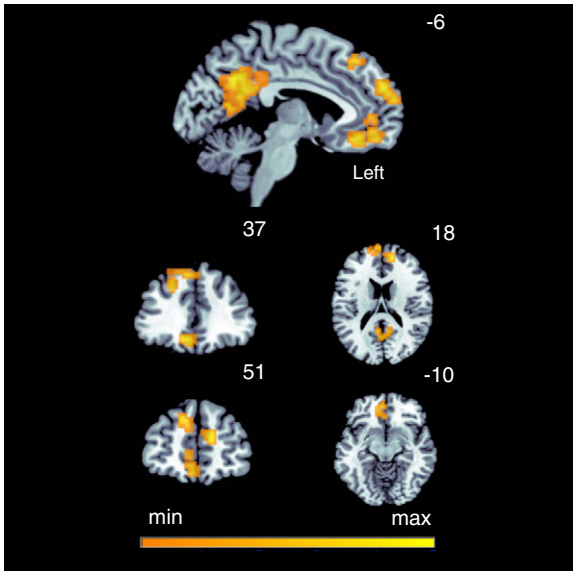

Fig. 1. Neural recruitment reflecting perceptually decoupled thought regardless of task relevance. The brain regions for which the correlation between longer RT and the bold signal was different when the perceptual input was important to actions (targets in the choice reaction time task, CRT, and the pre-target interval during working memory, WM) than when perceptual input was less important to actions (pre-target interval during CRT and targets during WM). Images were thresholded at $p<.005$. Minimum cluster size (k = 71) was determined using topological FDR.

Table 2
Regions of activation observed in the current experiment.

	t	Cluster size	Peak co ordinates		
			X	y	z
Posterior cingulate cortex/precuneus	4.69	255	−9	−58	34
MPFC	4.45	112	12	50	16
Dorsal MPFC	4.02	76	−6	32	48
Ventral MPFC	3.93	71	−6	38	−15

fMRI

Our analysis consisted of a whole brain search of the patterns of brain activity that relate to faster actions that are controlled by memory and slower responding when actions depend on immediate perceptual input. Following Weissman et al. (2006) we created subject-specific GLM to estimate beta weights for four conditions, including the target stimuli and a pre-target interval for both WM and CRT tasks. In order to explore baseline activity during the pre-target interval we placed a regressor 2.5 s before the non-colored stimulus that directly preceded a colored stimulus (e.g. prior to the information that should be encoded during the WM task). Modeling the pre-target period in this fashion allowed us to assess the impact of trial-by-trial changes in baseline activity that preceded all information that could contribute to a response in both tasks using an equal time window. We also modeled the onset of the colored stimulus to index target related activity. For both of these regressors RT was a parametric modulator at the first level. The parametric modulation of the regressors placed in the pre-target interval allowed us to use trial-by-trial changes in the subsequent speed of responding as a proximal measure of the information processes that were taking place in the pre-target period. The parametric modulation of the neural activity that occurs upon presentation of the target provides a proximal indicator for the neural processes that facilitate or impair current action. The canonical HRF was used to model the BOLD data. Finally, average beta weights across the two runs of each task were calculated, indicating the strength of the correlation between BOLD activity and RT for each task and each event type. Higher beta values indicated brain regions in which increased BOLD activity is associated with slower responses to targets, and thus compromised (less efficient) performance.

Average beta weight estimates of each participant's RT-correlated BOLD activity for each event type (*target/pre-target baseline*) in each task (*WM/CRT*) were submitted to a second level random-effects analysis using a 2×2 repeated measures ANOVA. Using the subject-specific average beta images from the first-level analysis, we calculated a contrast that weighted events positively when cognition depended upon perception (*CRT colored* and *WM baseline*) and negatively on situations when it did not (*CRT baseline* and *WM colored*). Whole brain analyses were conducted, and thresholded at $p<.005$, correcting for multiple comparisons using topological FDR (Chumbley et al., 2010). This analysis revealed four clusters of activity: one within the PCC and three within the mPFC. These clusters are displayed in Fig. 1 and reflect neural regions whose activation showed an interaction between relatively longer RT under conditions when cognition should be guided by perception and shorter RT when cognition was guided by information based on memory (see also Table 2).

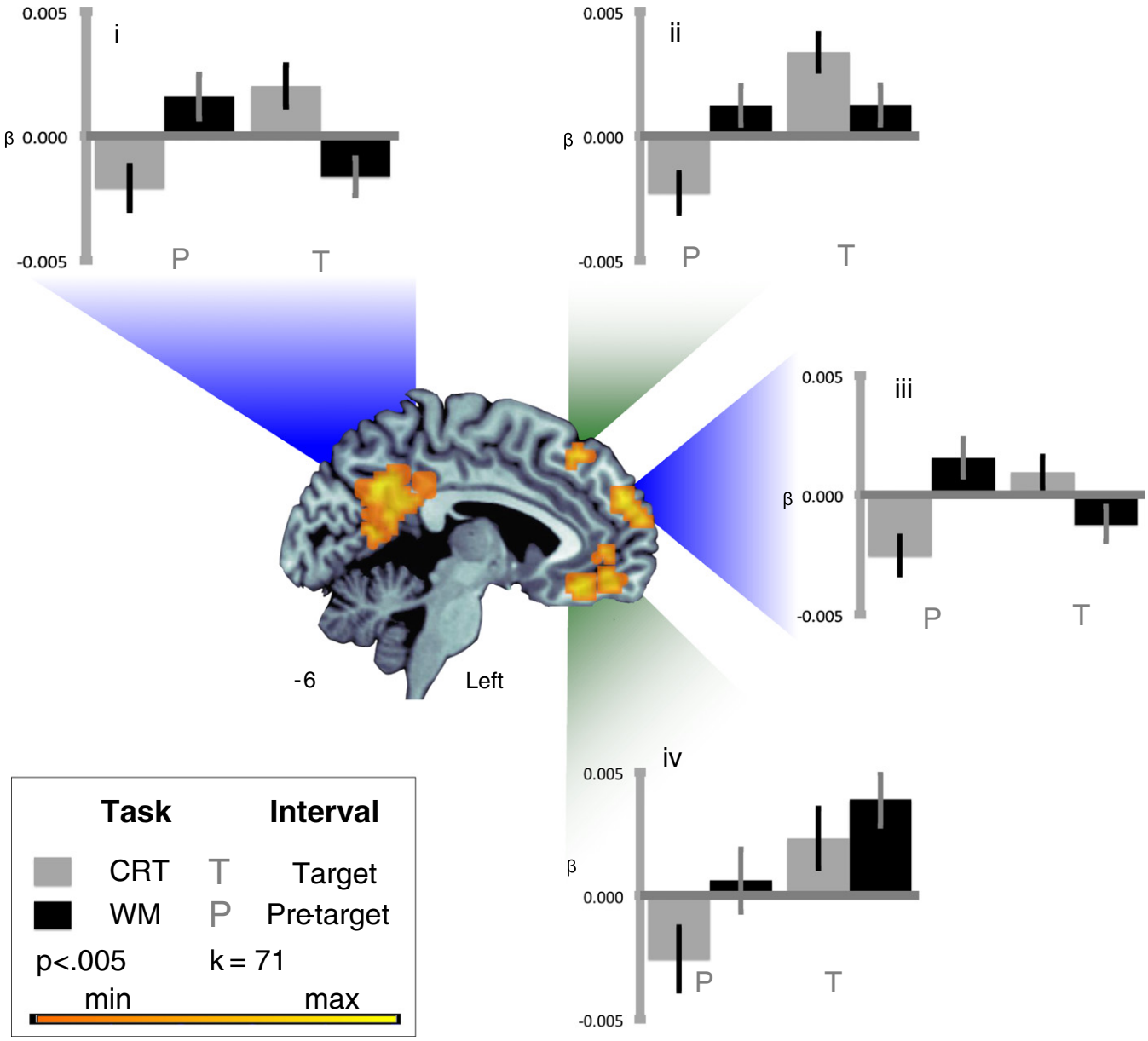

Fig. 2. Specific relation between RT and neural activity under conditions in which action depended on perceptual input or when it did not. Panels i–iv present the average beta weights at the group level in the peak voxels of each of the four clusters of activity demonstrating an interaction between RT when perception was more important to action and when it was less important to action. In both the posterior cingulate cortex (Cluster i) and medial pre-frontal cortex (Cluster iii) a full cross-over interaction was observed indicating that activity in these regions was associated with *faster actions* if task performance depended on memory and *slower actions* if task performance depended on perception. Regions: i) posterior cingulate cortex (PCC), ii) dorsal medial pre-frontal cortex (dMPFC), iii) medial prefrontal cortex (MPFC) and iv) ventral pre-frontal cortex (VMPFC).

To ascertain the specific nature of the relationship between neural activity and performance we extracted the average beta weights from the peak voxel in each of the four clusters. These were calculated separately for each task event (pre-target/target) in each task (CRT/WM) and are presented in Fig. 2. In the clusters centered around the PCC and the MPFC, indicated by the blue shading, neural activity and RT exhibited a complete cross-over interaction: in these regions higher BOLD signal activity was associated with faster actions when behavior did not depend on perception (e.g. the pre-target intervals in the CRT and the targets intervals in the WM task) and slowed responding when behavior depended directly on perceptual input (e.g. the pre-target intervals in the WM task and the targets in the CRT). In the clusters centered around the dorsal mPFC and in the ventral mPFC, indicated by green shading, the interaction was due to increased neural activity associated with longer RT whenever task relevant behavior depended on perception (e.g. the CRT). Only in the clusters in the PCC and the mPFC, therefore, was neural activity associated with a cost to actions based on perception as well as a benefit to actions based on memory.[1]

Finally, we used the default settings of SPM 8 to formally test the spatial conjunction null hypothesis (Nichols et al., 2005) between those brain regions that were associated with slower responding when action was based on immediate perceptual input and faster responding when action was based on information from memory.

[1] We also examined the reverse contrast (e.g. those brain regions which facilitated responding to external information and interfered with responding to internal information). This analysis yielded no clusters with sufficient extent to pass the cluster correction (FDR) when we applied the same threshold as in prior analyses ($p<.005$) nor an uncorrected threshold of $p<.001$.

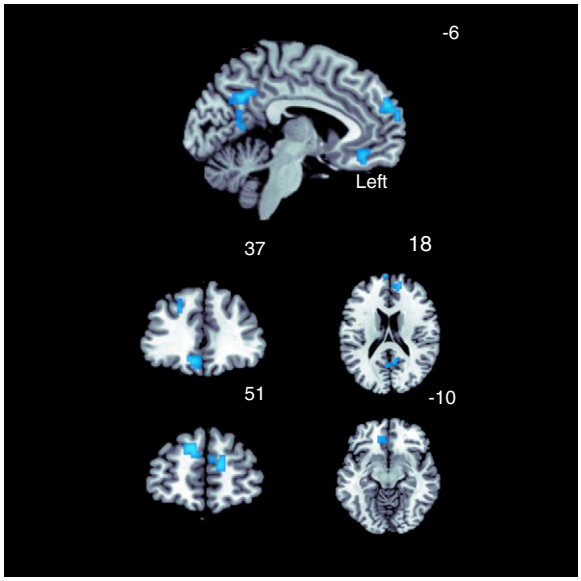

Fig. 3. The results of a conjunction analysis comparing the task differences in the correlation between RT and bold activity during targets (CRT>WM) and the pre-target interval (CRT<WM). Default SPM settings were used and the analysis was thresholded at $p<.05$. The minimum cluster size was set at 10.

The contrasts targets (CRT>WM) and non-targets (CRT<WM) were entered as the input images and the p-value for this conjunction was set at $p<.05$. The resulting images are presented in Fig. 3. For the purposes of display the minimum cluster size was set at 10. It can be seen that three of the four clusters identified by the main analysis exhibited activity in similar spatial regions. Importantly, therefore, the clusters of activity centered on the PCC and the mPFC – the two regions that exhibited a full crossover interaction in the main analysis – survived this more conservative conjunction analysis.

Discussion

The current work set out to identify whether elements of the DMN exhibit activity that support perceptually decoupled thought regardless of whether or not it resulted in immediate action. We observed clusters of activity in both the PCC and in a dorsal region of mPFC whose activity was associated with a faster responding to task relevant processing when behavior was governed by memory (e.g. responding during the WM task) and slower responding when behavior was controlled by immediate perceptual input (e.g. responding during CRT). Together these data suggest that cognitive operations that are engaged when the mind decouples attention from perceptual input occur in PCC and mPFC regardless of whether the ultimate cognitive goal is to perform an action in the here and now.

Although perceptually decoupled thought is necessary for certain forms of mental simulation, it can also derail the goals of the moment (see Smallwood, forthcoming-a, forthcoming-b for a discussion) and so the hypothesis that this information processing state is important for multiple psychological processes served by the DMN provides a simple parsimonious account for the variety of mental states that have been linked to this network. For example, prior studies have documented that elements of the default mode such as mPFC and pCC have been linked to absent-minded lapses (e.g. Christoff et al., 2009; Weissman et al., 2006). Others have documented higher DMN activity under situations in which internal guided thought is necessary such as during mental simulation or episodic retrieval (Huijbers et al., 2011; Mitchell, 2009; Mason et al., 2007). As both absent-minded lapses and mental simulation can depend on perceptual decoupling, the hypothesis that elements of the DMN affords perceptually decoupled thought not only accounts for the current data it also provides a unified account of the variety of psychological processes that are associated with this network.

We observed that regions in both the mPFC and pCC exhibit behavior that are consistent with the claim that they afford perceptually decoupled thought and this hypothesis gains further support from prior accounts of the specific function postulated for each region. For example, several authors have suggested that mPFC allows cognition to focus on internal representations rather than those provided by perception, perhaps by allowing the integration of multiple features in the services of a cognitive task (Christoff et al., 2004; Wagner et al., 2005). It has also been argued that the mPFC serves a general function that supports a retrieval mode that is independent of content (e.g. Tulving, 1987). Because the contents of the retrieval processes engaged during spontaneous self-generated thoughts are not likely to entail the parity of numbers, while task related retrieval in the WM tasks must, the overlap between these two conditions in mPFC is consistent with the view that this region supports a general purpose retrieval mode. Finally, there are several lines of anatomical evidence that supports a link between internally focused thought and the mPFC. In macaques the uncinate fasciculus fiber tract connects the mPFC to areas of the medial temporal lobe (Petrides and Pandaya, 2007) and resting state studies in humans has revealed functional connectivity between the bilateral hippocampus and ventral regions of mPFC (Kahn et al., 2008). Indeed, consistent with a role of the uncinate fasciculus in memory-guided thought, patient M.L., who suffered a focal lesion to this fiber tract was unable to engage in normal mental time travel (Levine et al., 1998). Together this functional and anatomical evidence suggests that MPFC receives input from brain systems that are known to represent information stored internally rather than sensory information and is one reason why this region may allow behavioral control that is independent of stimulus input and hence more abstract (Ramnani and Owen, 2004).

Our data also suggests that the pCC is important in processes necessary for perceptually decoupled cognition. Consistent with evidence for a role of the pCC in perceptual decoupling, studies using tasks that depend on control but with less requirement on memory retrieval (e.g. the Eriksen flanker task) have demonstrated that the pCC region increases activity when external task performance suffers (Eichele et al., 2008). Critically, however, pCC is also known to support task relevant memory retrieval, and is thought to be especially important in resolving the competition between memory retrieval and concurrent perceptual input. In a recent study, Huijbers and colleagues developed a paradigm in which the retrieval of information from memory occurs in the context of task irrelevant visual input. This study demonstrated that pCC activity is high when retrieval is successful and task irrelevant visual input is disregarded. By contrast, when pCC activity is low retrieval fails and the task irrelevant visual input is more likely to be encoded (Huijbers et al., 2009). This evidence suggests that pCC activity may be important in the resolution of competition between concurrent external input and memory retrieval processes and so could be important in stabilizing an internal train thought against the disruptions of the external environment (see Smallwood, forthcoming-b).

Based on these different lines of evidence we propose that these two regions of the DMN (pCC and mPFC) may serve complimentary functions in facilitating an internal train of thought; the mPFC may allow internal representations to influence cognition, whereas the pCC could help resolve the competition between external and internal information. Together the functions of perceptual decoupling as well as the self-generation of thought based on memory map directly onto theoretical formulations of those conditions that are conducive to the persistence of an internal train of thought that is unrelated to sensory input (Smallwood, forthcoming-a, forthcoming-b). If this

formulation is correct, understanding the interplay between pCC and mPFC may be important in attempts to understand cognition because the process of perceptual decoupling and coupling maybe involved in our capacity for freedom from immediacy that differentiates voluntary action from reflexive behavior (Haggard, 2008).

Finally, at the most general level these data add to a growing body of evidence (Spreng, 2012) that question the conception of the DMN as a *task-negative network* (Fox et al., 2005). Previous studies have argued against the idea that the DMN is necessarily anti-correlated with goal directed systems (such as the dorso-lateral PFC, or the dorsal anterior Cinglate Cortex) because both are active under certain conditions such as during mind-wandering (Christoff et al., 2009; Kirschner et al., 2012), autobiographical planning (Gerlach et al., 2011; Spreng et al., 2010; Spreng and Schacter, 2012) or when social information is maintained in working memory (Meyer et al., 2012). In a manner that is complimentary to the argumentation proposed by others (e.g. Spreng, 2012), the current study documents that the DMN provides support for perceptually decoupled thought if it occurs in the service of the task requiring memory input, while hindering task performance if activity in the same region occurs a few moments earlier in situations when perceptually coupled thought is important.

Although the coarse spatial resolution of fMRI means that we cannot preclude the possibility that specific populations of neurons serve distinct functions within different elements of the DMN, these data do indicate that at the network level the identification of whether a brain system serves to facilitate or interfere with a task cannot be made on brain anatomy alone. Instead, we propose that it is the temporal coupling of activity in brain regions to goals in the external environment that determines whether it helps or hinders concurrent actions (Smallwood et al., 2012a, 2012b, 2011a). Although the capacity for SIT allows us to perform goals based on long-term memory (Baird et al., 2011), is associated with delayed gratification, (Smallwood et al., in press) enhances creativity (Baird et al., 2012), and consolidates self-memories (Smallwood et al., 2011b, 2011c) its capacity to monopolize attention with unrelated information means it can also be the vehicle for absent-minded error (Barron et al., 2011; McVay and Kane, 2009). Based on the current result we suggest that absent-minded lapses do not necessarily depend upon specific neural processes, but rather occur in moments when the mind configures mental resources so as to perform an internal task that is incompatible with current behavioral goals (Smallwood, forthcoming-a, forthcoming-b). In this way our competence at perceptual decoupling comes with an associated cost: the capacity to escape from the constraints of the here and now facilitates the resolution of distant goals but does so at the detriment of the integrity of actions performed in the present.

Acknowledgments

This research was supported by supported by grant R305A110277 from the US Office of Education awarded to J.W. Schooler and J. Smallwood.

References

Andrews-Hanna, J.R., 2011. The brain's default network and its adaptive role in internal mentation. Neuroscientist.
Andrews-Hanna, J.R., Reidler, J.S., Sepulcre, J., Poulin, R., Buckner, R.L., 2010. Functional-anatomic fractionation of the brain's default network. Neuron 65 (4), 550–562.
Antrobus, J.S., Coleman, R., Singer, J.L., 1967. Signal-detection performance by subjects differing in predisposition to daydreaming. J. Consult. Psychol. 31 (5), 487–491.
Baird, B., Smallwood, J., Schooler, J.W., 2011. Back to the future: autobiographical planning and the functionality of mind-wandering. Conscious. Cogn.
Barron, E., Riby, L.M., Greer, J., Smallwood, J., 2011. Absorbed in thought: the effect of mind wandering on the processing of relevant and irrelevant events. Psychol. Sci. 22 (5), 596–601.
Buckner, R.L., Andrews-Hanna, J.R., Schacter, D.L., 2008. The brain's default network: anatomy, function, and relevance to disease. Ann. N. Y. Acad. Sci. 1124, 1–38.
Christoff, K., Ream, J.M., Gabrieli, J.D., 2004. Neural basis of spontaneous thought processes. Cortex 40 (4–5), 623–630.
Christoff, K., Gordon, A.M., Smallwood, J., Smith, R., Schooler, J.W., 2009. Experience sampling during fMRI reveals default network and executive system contributions to mind wandering. Proc. Natl. Acad. Sci. U. S. A. 106 (21), 8719–8724.
Fox, M.D., Snyder, A.Z., Vincent, J.L., Corbetta, M., Van Essen, D.C., Raichle, M.E., 2005. The human brain is intrinsically organized into dynamic, anticorrelated functional networks. Proc. Natl. Acad. Sci. U. S. A. 102 (27), 9673–9678.
Gerlach, K.D., Spreng, R.N., Gilmore, A.W., Schacter, D.L., 2011. Solving future problems: default network and executive activity associated with goal-directed mental simulations. NeuroImage 55 (4), 1816–1824.
Haggard, P., 2008. Human volition: towards a neuroscience of will. Nat. Neurosci. 934–946. http://dx.doi.org/10.1038/nrn2497.
Huijbers, W., Pennartz, C.M., Cabeza, R., Daselaar, S.M., 2009. When learning and remembering compete: a functional MRI study. PLoS Biol. 7 (1), e11.
Huijbers, W., Pennartz, C.M., Cabeza, R., Daselaar, S.M., 2011. The hippocampus is coupled with the default network during memory retrieval but not during memory encoding. PLoS One 6 (4), e17463.
Kahn, I., Andrews-Hanna, J.R., Vincent, J.L., Snyder, A.Z., Buckner, R.L., 2008. Distinct cortical anatomy linked to subregions of the medial temporal lobe revealed by intrinsic functional connectivity. J. Neurophysiol. 100 (1), 129–139.
Kirschner, A., Kam, J.W., Handy, T.C., Ward, L.M., 2012. Differential synchronization in default and task-specific networks of the human brain. Front. Hum. Neurosci. 6, 139.
Kleiner, M., Brainard, D., Pelli, D., 2007. What's new in Psychtoolbox-3? Perception 36 (ECVP Abstract Supplement).
Levine, B., Black, S.E., Cabeza, R., Sinden, M., McIntosh, A.R., Toth, J.P., Tulving, E., Stuss, D.T., 1998. Episodic memory and the self in a case of isolated retrograde amnesia. Brain 121, 1951–1973.
Mason, M.F., Norton, M.I., Van Horn, J.D., Wegner, D.M., Grafton, S.T., Macrae, C.N., 2007. Wandering minds: the default network and stimulus-independent thought. Science 315 (5810), 393–395.
McKiernan, K.A., Kaufman, J.N., Kucera-Thompson, J., Binder, J.R., 2003. A parametric manipulation of factors affecting task-induced deactivation in functional neuroimaging. J. Cogn. Neurosci. 15 (3), 394–408.
McKiernan, K.A., D'Angelo, B.R., Kaufman, J.N., Binder, J.R., 2006. Interrupting the "stream of consciousness": an fMRI investigation. NeuroImage 29 (4), 1185–1191.
McVay, J.C., Kane, M.J., 2009. Conducting the train of thought: working memory capacity, goal neglect, and mind wandering in an executive-control task. J. Exp. Psychol. Learn. Mem. Cogn. 35 (1), 196–204.
Mitchell, J.P., 2009. Social psychology as a natural kind. Trends Cogn. Sci. 13 (6), 246–251.
Nichols, T., Brett, M., Andersson, J., Wager, T., Poline, J.B., 2005. Valid conjunction inference with the minimum statistic. NeuroImage 25 (3), 653–660. http://dx.doi.org/10.1016/j.neuroimage.2004.12.005 (15).
Pelli, D.G., 1997. The VideoToolbox software for visual psychophysics: transforming numbers into movies. Spat. Vis. 10, 437–442.
Ramnani, N., Owen, A.M., 2004. Anterior prefrontal cortex: insights into function from anatomy and neuroimaging. Nat. Rev. Neurosci. 5 (3), 184–194.
Schacter, D.L., Addis, D.R., Buckner, R.L., 2007. Remembering the past to imagine the future: the prospective brain. Nat. Rev. Neurosci. 8 (9), 657–661.
Schacter, D.L., Addis, D.R., Buckner, R.L., 2008. Episodic simulation of future events: concepts, data, and applications. Ann. N. Y. Acad. Sci. 1124, 39–60.
Schacter, D.L., Addis, D.R., Hassabis, D., Martin, V.C., Spreng, R.N., Spuznar, K.L., 2012. The future of memory: remembering, imagining and the brain. Neuron 76, 677–694. http://dx.doi.org/10.1016/j.neuron.2012.11.001.
Shadlen, M.N., Gold, J.L., 2004. The neurophysiology of decision making as a window on cognition. In: Gazzaniga, M.S. (Ed.), The Cognitive Neurosciences III. MIT Press, pp. 1229–1243.
Smallwood, J., forthcoming. Distinguishing how from why the mind wanders: a process-occurrence framework for self-generated thought. Psychol. Bull.
Smallwood, J., forthcoming. Searching for the elements of thought: a reply to Franklin, Mrazek, Holloway and Schooler. Psychol. Bull.
Smallwood, J., Brown, K.S., Tipper, C., Giesbrecht, B., Franklin, M.S., Mrazek, M.D., et al., 2011a. Pupillometric evidence for the decoupling of attention from perceptual input during offline thought. PLoS One 6 (3), e18298.
Smallwood, J., Schooler, J.W., Turk, D.J., Cunningham, S.J., Burns, P., Macrae, C.N., 2011b. Self-reflection and the temporal focus of the wandering mind. Conscious. Cogn. 20 (4), 1120–1126.
Smallwood, J., Schooler, J.W., Turk, D.J., Cunningham, S.J., Burns, P., Macrae, C.N., 2011c. Self-reflection and the temporal focus of the wandering mind. Conscious. Cogn.
Smallwood, J., Brown, K., Baird, B., Schooler, J.W., 2012a. Cooperation between the default mode network and the frontal–parietal network in the production of an internal train of thought. Brain Res. 1428, 60–70.
Smallwood, J., Brown, K.S., Baird, B., Mrazek, M.D., Franklin, M.S., Schooler, J.W., 2012b. Insulation for daydreams: a role for tonic norepinephrine in the facilitation of internally guided thought. PLoS One 7 (4), e33706.
Spreng, R.N., 2012. The fallacy of a "task-negative" network. Front. Psychol. 3, 145.
Spreng, R.N., Stevens, W.D., Chamberlain, J.P., Gilmore, A.W., Schacter, D.L., 2010. Default network activity, coupled with the frontoparietal control network, supports goal-directed cognition. NeuroImage 53 (1), 303–317.
Stawarczyk, D., Majerus, S., Maj, M., Van der Linden, M., D'Argembeau, A., 2011. Mind-wandering: phenomenology and function as assessed with a novel experience sampling method. Acta Psychol. 136 (3), 370–381.
Tulving, E., 1987. Multiple memory systems and consciousness. Hum. Neurobiol. 6 (2), 67–80.
Wagner, A.D., Shannon, B.J., Kahn, I., Buckner, R.L., 2005. Parietal lobe contributions to episodic memory retrieval. Trends Cogn. Sci. 9 (9), 445–453.
Weissman, D.H., Roberts, K.C., Visscher, K.M., Woldorff, M.G., 2006. The neural bases of momentary lapses in attention. Nat. Neurosci. 9 (7), 971–978.