



Creating external reminders for delayed intentions: Dissociable influence on “task-positive” and “task-negative” brain networks



Julia Landsiedel, Sam J. Gilbert*

Institute of Cognitive Neuroscience, University College London, UK

ARTICLE INFO

Article history:

Accepted 8 October 2014

Available online 16 October 2014

Keywords:

Prospective memory
fMRI
Prefrontal
Distributed cognition
Memory aids
Theta

ABSTRACT

Studies of prospective memory and other paradigms requiring participants to remember delayed intentions typically reveal a distinction between lateral and medial rostral prefrontal cortex, whereby the experimental condition yields increased signal in the former region and decreased signal in the latter. These regions comprise nodes of larger “task-positive” and “task-negative” networks that often show opposite patterns of signal change in response to diverse cognitive demands. However, it is not clear to what extent activity in these networks is A) inverse but equivalent, or B) functionally dissociable. In order to address this question, participants performed an “intention-offloading” task while undergoing fMRI. On each trial they remembered a delayed intention, which they had the opportunity to fulfill after a brief filled delay. In one condition they were required to set an external reminder of this intention, while in the other they acted without any external memory aid. Results indicated a clear functional dissociation between the two networks. Compared with a control task with no delayed intention, there was a highly significant reduction in task-negative deactivation when participants used an external memory aid. However, there was no reduction in task-positive activation. These results are consistent with previous evidence that medial rostral prefrontal cortex plays a prominent role in representing the content of delayed intentions, accompanied by a reduction in BOLD signal and potentially increased theta-band oscillatory activity. This role is no longer required once an external reminder has been created. By contrast, lateral rostral prefrontal cortex may play a content-free role, unaffected by the offloading of content into the external environment.

© 2014 The Authors. Published by Elsevier Inc. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

Introduction

The past 15 years have seen rising interest in neuroimaging paradigms investigating participants' ability to fulfill delayed intentions (Burgess et al., 2001, 2003; Gilbert et al., 2009; Gilbert, 2011; McDaniel et al., 2013; Momennejad & Haynes, 2012, 2013; Okuda et al., 1998; Reynolds et al., 2009; Simons et al., 2006; reviewed by Burgess et al., 2011). A consistent finding across such studies has been that intention maintenance is associated with increased signal in lateral rostral prefrontal cortex (PFC) and decreased signal in medial rostral PFC, corresponding approximately with the lateral and medial aspects of Brodmann Area 10 respectively (Burgess et al., 2011). However, the origins of this lateral/medial distinction are not fully understood.

Similar results have been observed not just in the context of paradigms requiring memory for delayed intentions, but across a wide variety of experimental tasks. Thus, lateral and medial rostral PFC have been described as nodes within anticorrelated networks of brain regions, referred

to as A) “task-positive” or “multiple demand” (i.e. typically showing increased BOLD signal in experimental versus control conditions), and B) “task-negative” or “default” (i.e. typically showing reduced BOLD signal in experimental conditions) (Duncan, 2010; Fox et al., 2005). Although there is evidence that paradigms involving delayed intentions disproportionately yield activations within the most anterior portions of the PFC (Duncan, 2013; Gilbert et al., 2006a), these wider networks seem to operate across diverse cognitive domains, generally with opposite directions of signal change (though see Spreng, 2012). How might we explain this pattern?

One possibility might be that activity in task-negative regions such as medial rostral PFC does not play any functional role in the experimental tasks, and that activity in this network in fact reflects only mind-wandering and other task-unrelated processes (Andrews-Hanna et al., 2010; Mason et al., 2007). Such processes might be more common in low-demand (control) conditions than during experimental tasks (Antrobus, 1968; Teasdale et al., 1995). However, several lines of evidence argue against this possibility, at least insofar as it relates to medial rostral PFC. First, Gilbert (2011) showed, using multi-voxel pattern analysis (Norman et al., 2006) that patterns of activity in medial rostral PFC carry representational information specifying the content of delayed

* Corresponding author at: Institute of Cognitive Neuroscience, 17 Queen Square, London WC1N 3AR, UK. Fax: +44 20 7813 2835.
E-mail address: sam.gilbert@ucl.ac.uk (S.J. Gilbert).

intentions, indicating a role of this region in representing task-relevant information. Using a different paradigm, this finding was replicated in two studies by Momennejad and Haynes (2012, 2013). This would not be expected if activity in medial rostral PFC was characterized entirely by task-unrelated processes. Second, studies of patients with lesions wholly (Bird et al., 2004) or mostly (Uretzky & Gilboa, 2010) restricted to medial PFC reveal deficits on tasks requiring maintenance of delayed intentions such as the Six Element Test (Shallice & Burgess, 1991), again suggesting functional involvement of this region in the relevant tasks. Third, Gilbert et al. (2012b) found that task difficulty, as measured by response time and error rate, did not account for task-induced deactivation in medial rostral PFC. Activity in this region was enhanced in both an easy and a difficult perceptual task, compared with a condition of intermediate difficulty requiring stimulus-independent thought (i.e. cognitive processes uncoupled from the immediate sensory environment). These results rule out a simple model whereby medial rostral PFC activity is inversely related to task difficulty, as indexed by response time and error rate. Fourth, Gilbert et al. (2006b) found that medial rostral PFC activity was functionally related to task performance in a simple response time task, contrary to the predictions of an account supposing that this activity reflects distraction from the task at hand. Thus, the idea that activity in medial rostral PFC merely reflects task-unrelated thought associated with low-demand (or 'easy') conditions does not provide an adequate explanation of recent findings (although it may provide a partial explanation).

Such findings have been interpreted within the framework of the 'gateway hypothesis' (Burgess et al., 2007; Gilbert et al., 2005; Henseler et al., 2011), according to which lateral and medial rostral PFC play a role in promoting attention to stimulus-independent and stimulus-oriented thought respectively. Stimulus-independent thought refers to cognitive processes uncoupled from the immediate sensory environment, such as those required to maintain a pending intention, whereas stimulus-oriented thought refers to cognitive processes driven by current perceptual processing, such as those that may be involved in an ongoing task within which a delayed intention is embedded (Barban et al., 2013, 2014; Henseler et al., 2011). This hypothesis proposes that both lateral and medial rostral PFC play a role in participants' fulfillment of delayed intentions, acting together to modulate the balance between stimulus-independent and stimulus-oriented thought. This is proposed to facilitate the integration of ongoing task performance with the requirement to interrupt such performance in order to fulfill delayed intentions.

Another source of evidence for understanding the role of task-negative regions in cognitive tasks has come from the study of frontal midline theta oscillations (Hsieh & Ranganath, 2014). These are scalp recorded EEG fluctuations in the range of 4–8 Hz, which have been observed during working- and episodic-memory tasks and are typically maximal around the Fz electrode site. Studies acquiring simultaneous EEG and fMRI data have identified a robust relationship between frontal midline theta power and BOLD signal reduction in task-negative regions such as medial rostral PFC (Michels et al., 2010; Scheeringa et al., 2008, 2009; White et al., 2013). For example, Scheeringa et al. (2009) investigated a Sternberg working memory task, finding that there was a tight coupling between increased cognitive demand, increased frontal midline theta power, and reduced BOLD signal in regions such as medial rostral PFC. Consequently, they concluded that such data "strongly suggests that increased frontal theta EEG power can be regarded as a direct consequence of the decreased default mode network activity as measured by fMRI" (p. 1235). Likewise, White et al. (2013) concluded that in their fMRI-EEG study "it is likely that the frontal theta recorded currently has a medial frontal DMN [default mode network] source" (p. 2940; see also Michels et al., 2010 for a similar conclusion). Phillips et al. (2014) provided direct evidence in the macaque for a role of theta-band oscillations in cognitive control, with a medial frontal source. It is unclear why the increased theta power recorded with EEG should be accompanied by reduced BOLD signal recorded with fMRI,

but one possibility, supported by both theoretical and empirical arguments, is that periods of increased theta power may be accompanied by a decrease in power in higher frequencies such as gamma, and hence a net reduction in metabolic demand (Hsieh & Ranganath, 2014; Kilner et al., 2005).

According to both the gateway hypothesis and the "theta-induced deactivation" hypothesis, medial rostral PFC and other task-negative regions can play a functional role in certain experimental tasks, accompanied by decreased BOLD signal in the experimental condition. By contrast, task-positive regions – by definition – show increased BOLD signal during those conditions. However, it is not well understood to what extent BOLD responses in these systems should be seen as mirroring each other, i.e. inverse but equivalent, or functionally distinct.

One result suggesting functional divergence between lateral and medial rostral PFC comes from the study by Gilbert (2011) noted above. In this study, lateral rostral PFC showed enhanced BOLD signal while participants maintained delayed intentions. However, using multi-voxel pattern analysis it was not possible to decode the content of delayed intentions from this region, whereas it was possible to do so from medial rostral PFC. Thus, Gilbert (2011) proposed that, at least in some circumstances, lateral rostral PFC may play a content-free role in remembering delayed intentions, with their content represented in medial rostral PFC amongst other regions (though see also Momennejad & Haynes, 2012). According to this model, rather than merely mirroring each other, the two regions play functionally distinct roles when participants maintain delayed intentions. In the present study, this possibility is investigated further using an "intention-offloading" paradigm.

Intention offloading may be defined as the creation of an external trigger for a delayed intention, so that participants need not rely on a purely stimulus-independent representation of its content (Gilbert, *in press*). An everyday example might be the use of a diary or smartphone reminder to trigger prospective memory, or placing an object in a noticeable position to cue intended behavior at the appropriate time. Once an external cue of this sort has been set up, the need to maintain an internal representation of the delayed intention's content is reduced or eliminated. In a series of web-based experiments, Gilbert (*in press*; submitted) showed that intention offloading a) is influenced by task characteristics (i.e. participants are more likely to offload intentions when they have more to remember, or they are more likely to encounter interruption before being able to act); b) is influenced by metacognitive factors (participants who expected to perform poorly at the task made greater use of intention offloading and, independently, participants who objectively did perform poorly at the task made greater subsequent use of intention offloading); and c) improves performance: participants who offloaded their intentions were more likely to subsequently fulfill them. Furthermore, the web-based task investigated in these studies had better external validity for predicting fulfillment of a real-world task (visiting a specified web-link one week after the experiment) than more standard tests of prospective memory. However, the consequences of intention offloading at a neural level have not yet been investigated, despite the ubiquity of this strategy in everyday life.

In the present study, the intention-offloading task used by Gilbert (*in press*) was adapted for an fMRI testing environment, and compared against a control condition without any requirement to remember delayed intentions (see Fig. 1). In this task, participants drag a set of numbered circles in sequence to the bottom of a box, while remembering delayed intentions (e.g. drag 3 to the top instead). In some conditions, participants also have the option of setting a reminder at the beginning of the trial, e.g. by dragging the 3 circle to the top of the box at the beginning of the trial, so that its location cues the intended behavior at the appropriate time. Once reminders have been set up, there is no need to internally represent the content of delayed intentions seeing as this content is now represented externally. However, there may still be the requirement to remember that *something* needs to be done. Thus, while the representational content of the intention may have been offloaded, participants must still remember that they have an additional

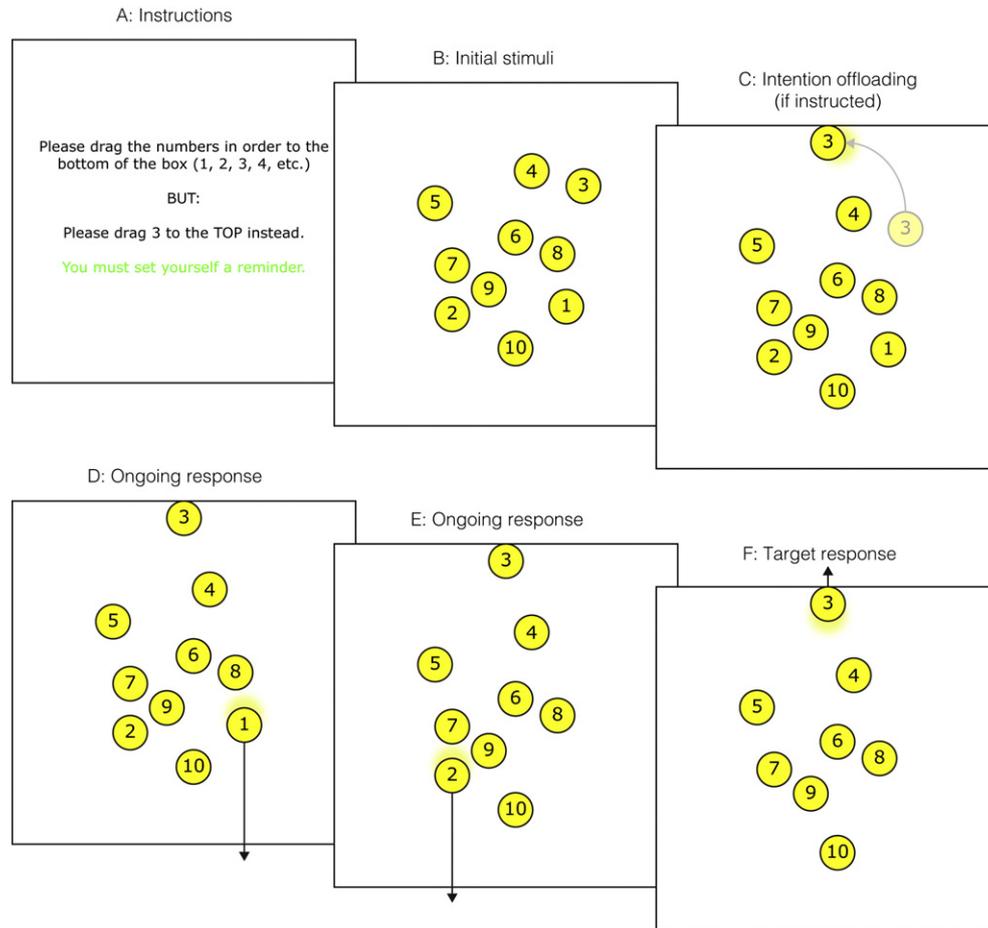


Fig. 1. Schematic illustration of one trial of the intention offloading task.

task demand. In this case, the putative content-free role of lateral rostral PFC might still be required, but not the content-representing role of medial rostral PFC (Gilbert, 2011). Therefore two hypotheses might be contrasted here. If activation profiles in lateral and medial rostral PFC are simply mirror images of each other then intention offloading might be expected to decrease both lateral rostral PFC activation and medial rostral PFC deactivation. However if medial, but not lateral, rostral PFC plays a prominent role in representing the content of delayed intentions, offloading might be predicted to preferentially influence activity in medial rostral PFC.

Methods

Participants

Sixteen right-handed participants were recruited (7 males; mean age: 22, range 19–32), one of whom was discarded due to excessive head movement, leading to a final sample of fifteen participants. The experiment was approved by the local ethics committee, and all participants provided written informed consent before taking part.

Intention-offloading task

The task was adapted from Gilbert (in press). On each trial, ten yellow circles numbered 1–10 were positioned randomly within a box (Fig. 1). Participants used a MRI-compatible trackball to drag the circles in turn (1, 2, 3 etc.) to the bottom of the box. Every time they did this, the circle turned purple and disappeared, leaving the other circles on the screen. After the 10th circle had disappeared, the screen was cleared

and the next trial began. For a demonstration, please visit "<http://www.ucl.ac.uk/sam-gilbert/demos/offloadMRIdemo.html>".

Alongside the 'no intention' control condition described above, in four other conditions participants were provided with delayed intentions. They were instructed to drag either one circle to a randomly selected alternative location, instead of the bottom of the box (e.g. drag 3 to the top), or three circles to the three alternative locations (e.g. drag 3 to the top, drag 7 to the left, drag 9 to the right). Thus, participants formed delayed intentions to perform particular actions when they encountered pre-specified cues, although they could produce a standard ongoing response (i.e. dragging the circle to the bottom of the box) if they forgot. When they correctly dragged a target circle to its instructed location, it turned green before disappearing; however, any other time a circle was dragged to the left, right, or top, it turned red before disappearing, thus providing feedback. On half of the trials, participants were required to set an external reminder in order to 'offload' their intentions. They did this by dragging the target circles towards their instructed locations at the beginning of the trial, so that their position would cue the appropriate response when they were reached in the sequence. From this point onwards, there is no requirement to internally represent the content of a delayed intention seeing as the placement of the circle itself represents this content. For the other trials, intention offloading was not permitted and only the upcoming circle in the sequence could ever be dragged; the other circles remained fixed in place (i.e. circle 2 could only be moved after circle 1 had disappeared; circle 3 could only be moved after circle 2 had disappeared, etc.) In order to ensure that participants offloaded intentions when it was permitted, on these trials the first circle could only be removed from the screen after all target circles had first been moved elsewhere in the box. Thus, in total there were five conditions: no intention, offload

1, offload 3, no offload 1, and no offload 3. The target circles were randomly selected between the 3rd and 10th in the sequence.

Each trial began with a 7 s instruction period, where participants were informed of any targets for that trial and also (apart for the 'no intention' condition) whether they would be required to offload intentions. This was specified with either the message "You must set yourself a reminder" or "You will not be able to set yourself a reminder" in green or red respectively. Following the instruction period, the trial began immediately, and continued in a self-paced manner until the 10th circle had been removed from the screen. This was followed by a blank screen for 4 s and then, if there was a minimum of 20 s remaining in the scanning run, the instructions for the next trial.

One third of trials belonged to the no intention condition; other trials were divided evenly between the other four conditions. The ordering of these trials was determined by generating 20,000 random trial sequences and testing the resulting design matrices (using self-paced timings drawn from behavioral pilot data) for the efficiency of the contrasts of interest (Henson, 2007). The most efficient sequences were then used, with a fresh sequence for each run and each participant. In practice, this ensured that every third trial belonged to the no intention condition, followed by two trials drawn from the other four conditions, where each condition differed from the preceding one.

Procedure/MRI scanning

Participants were first familiarized with the task and the trackball in a 5–10 minute practice session outside the scanner. Following this, a 1.5 T Siemens TIM Avanto scanner with 32-channel head coil was used to acquire both T1-weighted structural images and T2*-weighted echoplanar images (64 × 64; 3.5 × 3.5 mm pixels; echo time, 40 ms) with blood oxygen level-dependent (BOLD) contrast. Each volume comprised 31 axial slices (3.5 mm thick, oriented approximately to the anterior commissure–posterior commissure plane), covering most of the brain but omitting inferior portions of the cerebellum. Functional scans were acquired in four sessions, each comprising 228 volumes (~9.5 min). Volumes were acquired continuously with an effective repetition time of 2.5 s per volume. The first four volumes in each session were discarded to allow for T1 equilibration effects. Between the second and third functional scans, a 6 min T1-weighted MPRAGE structural scan was collected.

Data analysis

MRI data were analyzed using SPM8 software (<http://www.fil.ion.ucl.ac.uk/spm/software/spm8/>). The volumes were realigned and corrected for different slice acquisition times. They were then normalized into 3 mm cubic voxels with fourth-degree B-spline interpolation using normalization parameters derived from segmentation of the co-registered structural scan, then smoothed with an isotropic 8 mm full-width half-maximum Gaussian kernel. The volumes acquired during the four sessions were treated as separate time series. For each series, the variance in the BOLD signal was decomposed with a set of regressors in a general linear model.

10 boxcar regressors were generated to code for 1) the instruction period for each trial, separately for each of the five conditions, and 2) the task period for each trial, again separated by the five conditions. Furthermore, a single additional regressor was generated, comprised of delta functions representing effects of no interest, specifically a) target miss trials (i.e. dragging a target to the bottom of the screen), and b) false alarm/error trials (i.e. dragging a non-target to the left, right, or top, or a target to the wrong location). These regressors were convolved with a canonical hemodynamic response function. In a separate additional model, the five conditions were modeled with finite impulse response (FIR) regressors. Each condition was modeled from the instruction period onwards with a set of 14 regressors, each representing a 2.5 s (i.e. 1 TR) time period. This allowed the temporal

dynamics of the BOLD responses to each condition to be examined. The regressors outlined above, along with regressors representing residual movement-related artifacts and the mean over scans comprised the full model for each session. The data and model were high-pass filtered to a cutoff of 1/128 Hz.

Parameter estimates for each regressor were calculated from the least mean squares fit of the model to the data. Effects of interest were assessed in a random-effects analysis by first forming subject-specific contrasts subtracting the no intention condition from each of the other four conditions in turn. The four resulting contrast images were entered into a repeated-measures ANOVA using nonsphericity correction (Friston et al., 2002), representing the factorial crossing of number of targets (1, 3) and offloading (yes, no). Results are reported applying a height threshold of $p < .005$ uncorrected in conjunction with an extent threshold determined by SPM8 to achieve $p < .05$ familywise error correction for multiple comparisons across the whole brain volume. Region of interest (ROI) analyses were conducted by extracting subject-specific contrast estimates from the relevant ROIs with custom Matlab code, then entering the resulting data into repeated measures ANOVAs with SPSS (version 22 for Mac OS).

Results

Behavioral results

The mean number of completed trials was 15.7 (range: 13–19) in the no intention condition, and 8.0 (range 5–11) for the other four conditions. Mean trial durations were 30 s, 35 s, 44 s, 30 s, and 33 s in the no intention, offload 1, offload 3, no offload 1, and no offload 3 conditions respectively (note that trial durations in the offload conditions were longer than the no offload conditions due to the time spent creating reminders at the beginning of the trial). The mean proportion of target circles dragged to their instructed locations were .99, .95, .97, and .95 in the offload 1, offload 3, no offload 1, and no offload 3 conditions respectively (main effect of 1 vs 3 targets: $F(1,14) = 6.1$, $p = .03$; main effect of offloading / offloading × targets interaction: $F(1,14) < 1.5$, $p > .25$). False alarms (i.e. dragging a nontarget circle to one of the three target locations) were rare (<1%). Note that the present experimental paradigm was not optimized for sensitivity to behavioral effects; for further exploration of such effects see Gilbert (in press; submitted).

fMRI results

In order to localize regions showing BOLD signal increases or decreases associated with the delayed intention conditions, the four experimental conditions were collapsed and compared against the 'no intention' control condition, i.e. using a contrast of [1 1 1 1] for the offload 1, offload 3, no offload 1, and no offload 3 conditions, each of which represented a subtraction between the relevant condition and the no intention control condition. Regions of significant signal change are shown in Fig. 2 and Table 1. Five clusters showed increased signal during the delayed intention conditions: bilateral dorsolateral PFC (BA 46/10), bilateral posterior frontal cortex (BA 6/8) and a single cluster in superior parietal cortex, extending bilaterally along the intraparietal sulcus (BA 7/40). BOLD signal decreases associated with the reverse contrast were seen in five clusters: medial frontal cortex (BA 8/9/10), posterior cingulate cortex (BA 23/30), left lateral occipito-temporo-parietal cortex (BA 37/39), and bilateral inferior temporal cortex (BA 20/21). These results fit well with previous descriptions of task-positive/task-negative networks (Buckner et al., 2008; Duncan, 2010). They are also consistent with previous studies of delayed intention tasks in revealing opposite patterns of signal change within lateral versus medial BA 10 (Burgess et al., 2011). To ensure adequate control of type-1 errors, the AlphaSim tool included in AFNI (<http://afni.nimh.nih.gov/afni/>) was used to provide Monte Carlo simulations of the probability of obtaining clusters of the observed sizes, given the spatial correlation across voxels estimated

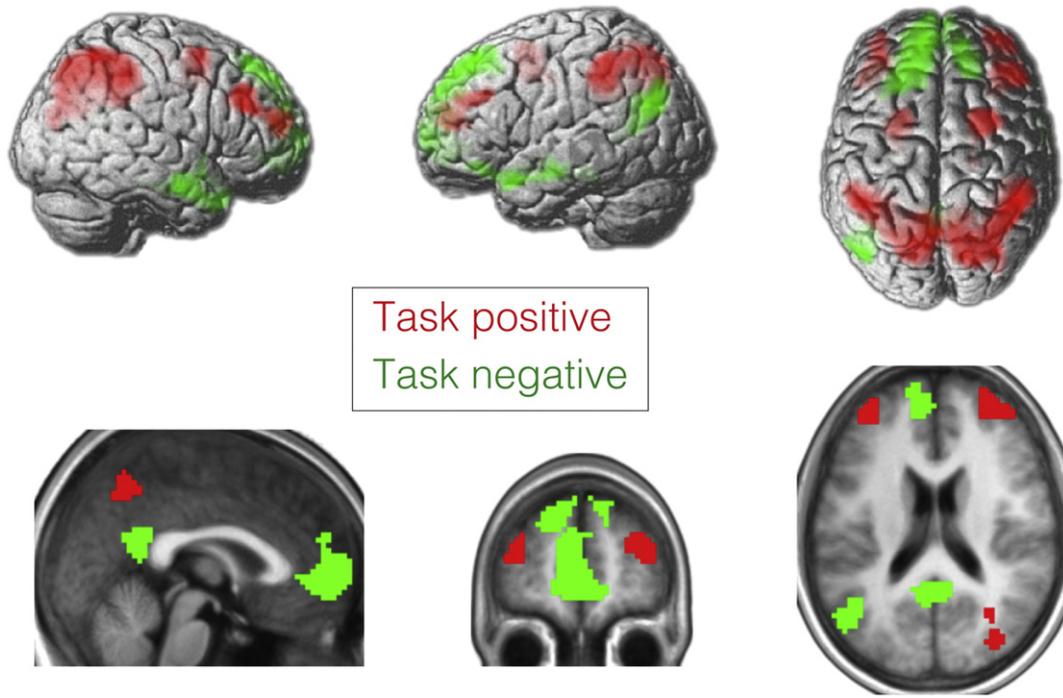


Fig. 2. Regions of significant signal change in the task-positive contrast of delayed intention > control (red) and task-negative contrast of control > delayed intention (green). Top: three-dimensional renderings of results on left hemisphere, right hemisphere, and superior views. Bottom: significant results plotted on sagittal ($x = 0$), coronal ($y = 54$), and axial ($z = 20$) views of the mean normalized structural scan.

from the residuals of the second-level SPM analysis. In every case, the observed cluster sizes were obtained with a probability below 0.05.

Region of interest analyses

In order to investigate potential differences between the four delayed intention conditions, results were analyzed using a region of interest (ROI) approach. This allows signal change in the conditions of interest to be examined within functionally defined regions, without requiring correction for multiple comparisons across the whole brain volume. ROIs were defined by the task-positive and task-negative analyses described above, collapsing across the four delayed intention conditions. These ROIs were then interrogated for signal change between these four conditions. Seeing as the ROI-defining contrasts

were orthogonal to the hypothesis-testing contrasts, these analyses were unbiased (Kriegeskorte et al., 2009). Separate analyses were performed for the task-positive and task-negative regions. These analyses allowed investigation of signal change across functionally-defined networks encompassing multiple brain regions, to see whether these networks showed a significant effect of Targets (one or three) and/or Offloading, collapsing across the various regions. For a conceptually-related example investigating the brain’s ‘mentalizing network’ see White et al. (2014). Seeing as Region was included as a factor in these analyses, any Region \times Contrast interactions could then be followed up in region-specific analyses. For the task-positive regions, which included bilateral pairs of clusters in lateral PFC and posterior PFC, along with a single parietal cluster encompassing both hemispheres, the parietal region was split into a pair of unilateral clusters and results were analyzed in a Region (3) \times Hemisphere (2) \times Offloading (2) \times Targets (2) repeated-measures ANOVA. For the task-negative regions, which included a set of midline clusters and lateral clusters that were not fully symmetrical, results were analyzed in a Region (5) \times Offloading (2) \times Targets (2) ANOVA. For both analyses, data from each ROI were first normalized into Z scores so that results were driven by condition-specific effects rather than overall differences in signal intensity between regions (caused, for example, by the higher signal intensity recorded from peripheral regions of the brain with a 32-channel head coil). Results are summarized in Fig. 3.

Table 1

Regions of increased signal (task-positive) and decreased signal (task-negative) in the delayed intention conditions, relative to the no-intention control condition (BA = Brodmann Area).

Region	BA	Peak co-ordinate	Z _{max}	N voxels
<i>Delayed intention > control (i.e. task positive)</i>				
Bilateral superior parietal cortex/ intraparietal sulcus	7/40	9, -61, 49	6.45	2820
R posterior frontal cortex	6/8	27, 5, 58	5.34	264
L posterior frontal cortex	6/8	-24, 5, 43	4.66	210
R lateral frontal cortex	46/10	36, 32, 31	4.22	324
L lateral frontal cortex	46/10	-36, 44, 28	4.30	196
<i>Control > delayed intention (i.e. task negative)</i>				
Medial frontal cortex	8/9/10	-18, 38, 49	5.32	1166
L temporo-parietal cortex	37/39	-48, -76, 31	4.80	220
L inferior temporal cortex	20/21	-33, 35, -14	4.63	436
Posterior cingulate	23/30	-9, -52, 7	4.59	253
R inferior temporal cortex	20/21	24, -13, -20	4.14	395

Task-positive network

In the task positive regions, there was a significant main effect of Targets, indicating increased signal change for three targets versus one target ($F(1,14) = 28.6, p = .0001, \eta^2 = .67$). The main effect of Offloading was not significant ($F(1,14) = 1.1, p = .31, \eta^2 = .07$), nor was the Offloading \times Targets interaction ($F(1,14) = .44, p = .52, \eta^2 = .03$). Thus, in the task positive regions, signal change was greater on trials with three targets than one target, but there was no significant influence of whether or not participants set external reminders. Although the

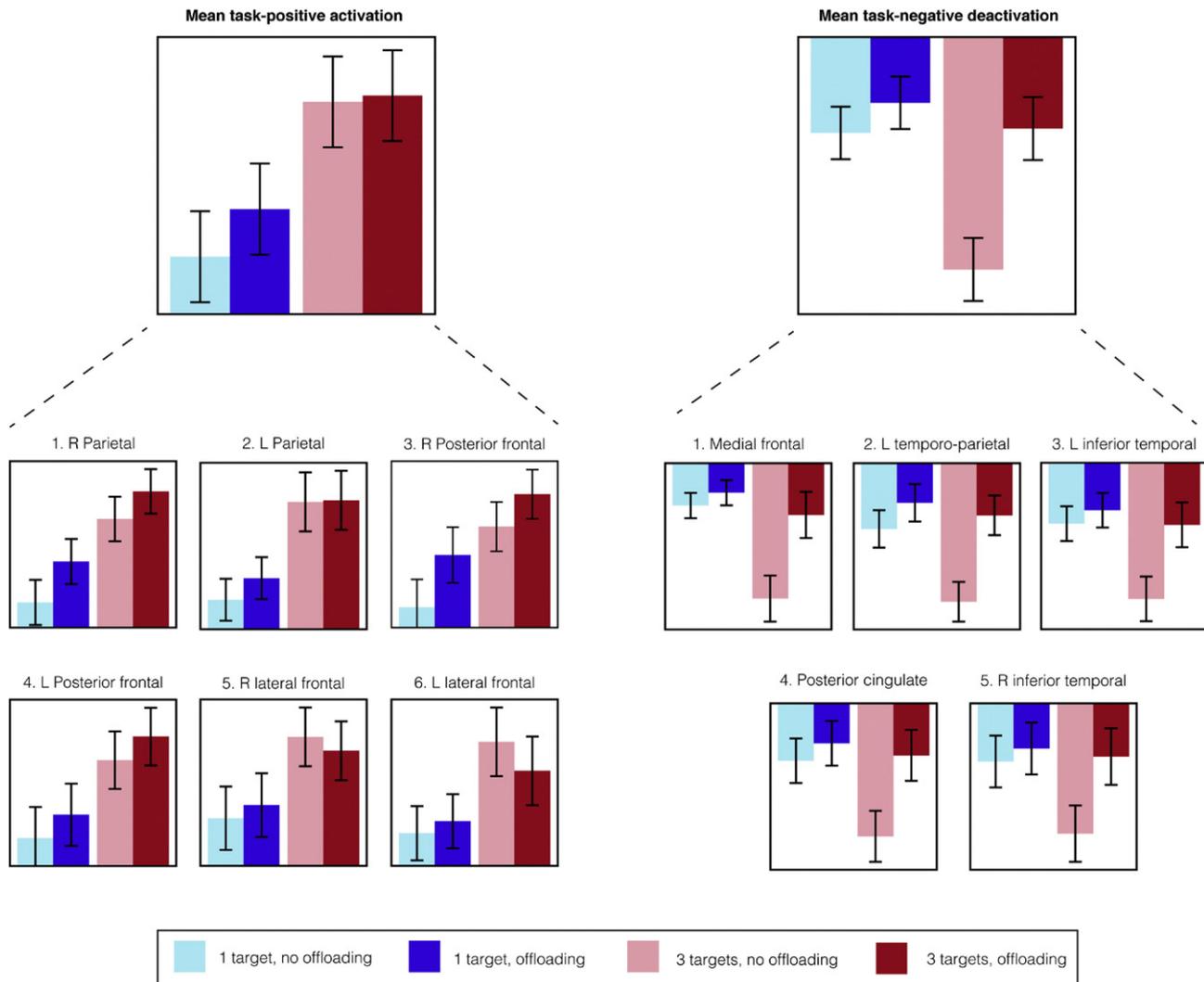


Fig. 3. Contrast estimates for each of the four experimental conditions in comparison with the control condition, in regions of interest defined by the task-positive and task-negative contrasts shown in Table 1. Error bars indicate 95% confidence intervals for the within-subject comparisons between offloading and non-offloading versions of the relevant condition, calculated such that the effect of offloading is significant ($p < .05$) when the bars do not overlap. Results are shown in arbitrary units, with the zero point (i.e. control condition) indicated by the bottom of the box for task-positive graphs and the top of the box for task-negative graphs.

main effect of Offloading was not significant, there was a significant Region \times Offloading interaction ($F(2,28) = 4.1, p = .04, \eta^2 = .39$), and a significant Hemisphere \times Offloading interaction ($F(1,14) = 8.3, p = .01, \eta^2 = .37$), suggesting that intention offloading may have had an effect that differed between ROIs. Considering each ROI individually, the main effect of Offloading and the Offloading \times Targets interaction was nonsignificant in all regions ($F(1,14) < 1.6, p > .22, \eta^2 < .11$), with the exception of the right posterior frontal cortex cluster, which showed a significant effect of Offloading ($F(1,14) = 5.7, p = .03, \eta^2 = .29$), and right parietal cortex, which showed a marginally significant effect of Offloading ($F(1,14) = 4.4, p = .054, \eta^2 = .24$). Note however that neither of these effects was significant after Bonferroni correction for multiple comparisons across six ROIs. Rather than indicating a reduction in activity when external reminders were created, these effects reflected an increased BOLD signal, potentially due to additional demands associated with the requirement to set up an external reminder to begin with. In sum, while the task positive regions showed a clear increase in signal when there were three targets to be remembered rather than one (a finding that was significant in all six ROIs, $F(1,14) > 8.7, p < .011, \eta^2 > .38$), there was no evidence that signal in these regions was reduced

when an external reminder was available; if anything signal was increased in the offloading conditions.

Task-negative network

Turning now to the task-negative regions, there was again a significant main effect of Targets ($F(1,14) = 7.7, p = .01, \eta^2 = .35$), indicating increased deactivation (i.e. lower BOLD signal) for three targets versus one target. There was also a significant main effect of Offloading ($F(1,14) = 11.8, p = .004, \eta^2 = .46$), indicating reduced deactivation when intentions were offloaded, along with a significant Offloading \times Targets interaction ($F(1,14) = 13.0, p = .002, \eta^2 = .50$). These effects were consistently significant within all five regions ($F(1,14) > 4.7, p < .047, \eta^2 > .25$), with the exception of the main effect of Targets in the posterior cingulate ROI and the main effect of Offloading in the right inferior temporal ROI, both of which just missed significance ($F(1,14) > 4.0, p < .065, \eta^2 > .22$). There was a marginally significant Region \times Targets interaction ($F(4,11) = 3.2, p = .055, \eta^2 = .54$) but no significant Region \times Offload interaction ($F(4,11) = .2, p = .94, \eta^2 = .07$). Follow-up tests showed that the Offloading \times Targets interaction resulted from a significant effect of Offloading when there were

three targets ($F(1,14) = 19, p = .0005, \eta^2 = .59$) but not when there was one target ($F(1,14) = .5, p = .49, \eta^2 = .03$). Thus, whereas there was no evidence that activation in task positive regions was reduced by the use of external reminders, task-negative deactivation was reduced, at least when the memory load was higher.

Differential profile of activation between task-positive and task-negative networks

In order to test formally for a differential profile of activation between task-positive and task-negative regions, a single analysis was conducted combining results across both networks. First, results were averaged across all ROIs, separately for the two networks (positive, negative) and the four delayed intention conditions. Next, the sign of the task-negative parameter estimates was reversed, so that higher positive values indicated a larger deviation from baseline, as in the task-positive network. Without this step, a differential profile between the two networks might result, trivially, from their opposite directions of signal change. The parameter estimates for each network were normalized into Z scores (mean: 0, standard deviation: 1) so that they were matched in magnitude. Finally, the resulting data were entered into a Network (positive, negative) \times Offloading (yes, no) \times Targets (1, 3) repeated-measures ANOVA. This revealed a significant main effect of Targets ($F(1,14) = 45, p = .00001, \eta^2 = .76$), reflecting greater deviation from baseline in 3-target versus 1-target trials. The Network \times Targets interaction was not significant ($F(1,14) = 1.3, p = .28, \eta^2 = .08$). Thus, the response of task-positive and task-negative networks to the Targets manipulation was inverse but statistically equivalent. There was no significant main effect of Offloading ($F(1,14) = 2.7, p = .12, \eta^2 = .16$) but the Network \times Offloading interaction was significant ($F(1,14) = 7.1, p = .02, \eta^2 = .34$). This reflects the significant effect of Offloading on the task-negative but not task-positive network. Thus, the differential effect of intention offloading on task-positive and task-negative networks was statistically confirmed. The three-

way interaction of Network \times Offloading \times Targets was not significant ($F(1,14) = .9, p = .37, \eta^2 = .06$).

Lateral vs medial PFC

The analyses above considered the task-positive and task-negative networks as a whole. However, seeing as the lateral/medial PFC split is of particular theoretical importance, the forgoing analysis was also repeated for just the anterior PFC regions. This revealed a marginally significant Network \times Offloading interaction ($F(1,14) = 4.0, p = .065, \eta^2 = .22$). Thus, results were consistent with a differential profile between lateral and medial PFC regions. However, seeing as this conclusion rests on a marginally-significant result, the evidence for differential profiles appears stronger when considering the task-positive and task-negative networks as a whole. As before, there was no significant Network \times Offloading \times Targets interaction ($F(1,14) = 1.0, p = .34, \eta^2 = .06$).

FIR results

In order to evaluate the time course of task-positive activation and task-negative deactivation, a FIR analysis was conducted and parameter estimates were extracted for the four conditions, representing the period from the presentation of instructions onwards (with a total duration of 14 TRs covering 35 s). These results are summarized in Fig. 4, with results collapsed across all regions within the task-positive or task-negative networks (see Fig. S1 for results from each individual ROI). The shaded areas indicate 95% confidence intervals for the within-subject comparison between the offloading and non-offloading versions of the relevant condition, calculated so that the effect of offloading is significant ($p < .05$) when the shaded areas do not overlap. Note that it is unsurprising that the task-positive regions show above-baseline and the task-negative regions below-baseline activity, seeing as the ROIs were defined on the basis of this finding. However, the ROIs were defined independently of the offloading/non-offloading distinction, making the comparison between these conditions unbiased.

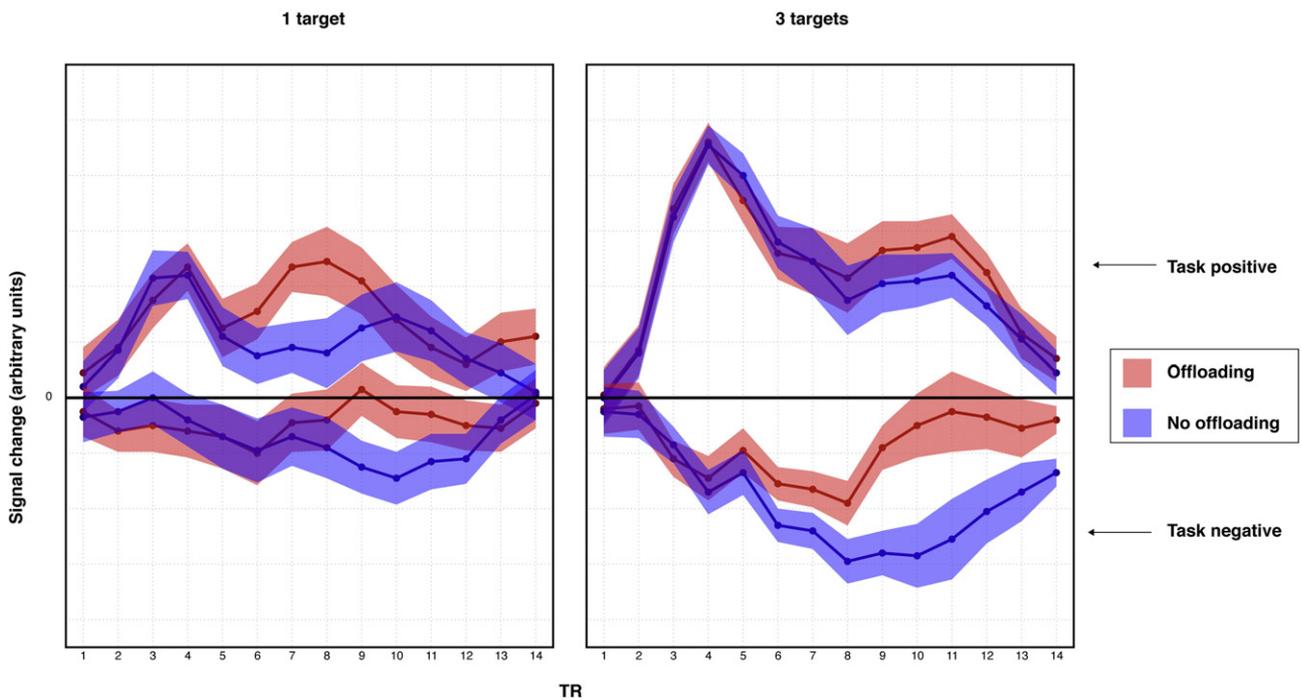


Fig. 4. Timecourse of task-positive and task-negative signal change in each of the four conditions, relative to the control condition. Shaded regions indicate 95% confidence intervals for the within-subject comparison between the offloading and non-offloading versions of the relevant condition, calculated such that the effect of offloading is significant ($p < .05$) when the shaded areas do not overlap.

In the 3-target conditions, task-positive regions show an increase in signal on presentation of the instructions, which then drops to an intermediate level during the task execution phase before dropping towards baseline. This pattern is statistically equivalent in the offloading and non-offloading conditions. By contrast, task negative regions initially show a similar deactivation in the offloading and non-offloading conditions, before rapidly returning towards baseline in the offloading condition but with a more pronounced deactivation in the non-offloading condition, leading to a significant difference between the two conditions at TRs 6–14. This suggests that deactivation in the task-negative regions at least partially reflects the requirement to maintain a representation of the content of delayed intentions, which is reduced after it has been offloaded. By contrast, the task-positive regions show no reduction in signal after intention offloading.

In the 1-target non-offloading condition, task-positive regions show an initial increase in signal, which drops to an intermediate level before eventually returning to baseline. The timecourse in the offloading condition is similar, with the exception of an additional peak that appears in TRs 7–8 leading to a significant difference between the two conditions at these timepoints. This difference should be interpreted with caution seeing as it was not observed in the main fMRI analysis reported above and is derived from multiple comparisons across 14 TRs. However, it would be consistent with additional activity associated with setting external reminders, then switching back to the ongoing task. In the task-negative regions, signal is initially decreased before returning to baseline in the offloading condition, with a more pronounced deactivation in the non-offloading condition in TRs 9–10. This pattern is similar to the one observed in the 3-target conditions, suggesting that intention offloading reduced task-negative deactivation in both the 1-target and 3-target conditions, even though this effect was only significant for the 3-target condition in the main analysis. Furthermore, the apparent lag between the effect of offloading seen at TRs 7–8 in the task-positive network, followed by an effect at TRs 9–10 in the task-negative network, would be consistent with the hypothesis that the task-positive effect reflects the act of setting up external reminders, followed by a task-negative reduction in deactivation once the intention has been offloaded.¹

Discussion

This study investigated the influence of external reminders on brain activity associated with briefly remembering delayed intentions. A network of 'task-positive' regions showed increased BOLD signal when participants remembered delayed intentions, while 'task-negative' regions showed decreased signal. When participants set external reminders, deactivation in task-negative regions was strongly reduced, at least when there was a larger memory load. However, there was no offloading-related reduction in task-positive activation; if anything there was an increased signal associated with setting external reminders. Thus, there was a qualitative difference between the activation profile of task-positive and task-negative regions. Rather than playing inverse but equivalent roles, the two networks were functionally distinct.

In the present study, there was no significant behavioral effect of the offloading manipulation, despite its clear impact on underlying brain activity (at least with respect to the task-negative network). This suggests that in some contexts, different patterns of underlying brain activity can yield similar overt behavior. However, for evidence from related

paradigms demonstrating the impact of intention offloading on behavioral accuracy, see Gilbert (submitted; in press).

Previous neuroimaging studies of delayed intention tasks have implicated rostral PFC (Burgess et al., 2011) but they have typically confounded 1) the requirement to maintain a preparedness to interrupt an ongoing task in order to fulfill a delayed intention, and 2) the requirement to maintain a representation of the intended behavior in working memory. The present results suggest that these two requirements can be preferentially linked to lateral and medial rostral PFC respectively. These results cannot be attributed to a general difference between task-positive and task-negative networks in the magnitude of their response to any cognitive demand (e.g. due to a difference in neurovascular coupling). When activity in the two networks was transformed into equivalent units (i.e. normalized difference from baseline), both networks showed an equivalent response to the 3- versus 1-target manipulation. However, the offloading manipulation clearly dissociated the two networks.

In the present study, BOLD signal was higher in task-negative regions when participants set external reminders, consistent with the suggestion from Gilbert et al. (2009) that medial rostral PFC activity is associated with externally-cued rather than self-initiated realization of delayed intentions. The most obvious consequence of setting an external reminder is that there is no need to maintain an internal representation of the content of a delayed intention. Once the reminder has been created, this content is physically represented in the world. Thus, task-negative deactivation appears to be associated with the requirement to maintain a representation of task-relevant information in working memory. This interpretation is consistent with studies of frontal midline theta oscillations, which have reported both decreased BOLD signal in task-negative regions, and an associated increase in frontal midline theta power, associated with increasing working memory demands (Michels et al., 2010; Scheeringa et al., 2009). Moreover, theta oscillations have been proposed to play an especially prominent role in multi-item working memory tasks, especially when temporal order information needs to be maintained (Hsieh et al., 2011), and potentially with representations of different memory items active at different phases of the theta cycle (Jensen & Lisman, 1998; Lisman & Idiart, 1995). This would be consistent with the stronger effect of offloading on 3-target than 1-target trials. The idea that task-negative regions can play a role in representing the content of delayed intentions is also supported by studies from multivariate pattern analysis of fMRI data, which have consistently shown that task-relevant representational content can be decoded from medial rostral PFC, a prominent node of the task-negative network (Gilbert et al., 2012a; Gilbert, 2011; Momennejad & Haynes, 2012, 2013). These findings are incompatible with the idea that activity in medial rostral PFC is characterized entirely by task-unrelated processes.

By contrast, lateral rostral PFC, a node of the task-positive network, has been proposed to play a content-free role in delayed intention tasks, at least under some circumstances (Gilbert, 2011). If this region does not play a role in representing the content of delayed intentions, there is no reason for its activation to be diminished when that content no longer needs to be represented. Instead, in paradigms such as the present experimental task, lateral rostral PFC might play a general of maintaining a preparedness to act on a delayed intention, the content of which is represented elsewhere, either in other brain regions or physically in the world. A similar proposal has been made on the basis of primate electrophysiology that lateral prefrontal regions do not necessarily themselves represent task-relevant content in a working memory task, but instead may implement a pointer to the relevant representation (Lara & Wallis, 2014). Of course, this does not rule out the possibility that lateral prefrontal cortex may play a role in representing task-relevant content in other experimental paradigms, such as those requiring continuous variables to be represented in terms of categorical boundaries (Freedman et al., 2001; Lee et al., 2013).

¹ One interpretation of the present results might be that intention offloading reduced task-positive activation, but this effect was masked by an increase in activation related to initially setting up the external reminders. In order to investigate this possibility, an additional analysis was conducted in which the initial intention-offloading period was modeled separately from the subsequent intention maintenance period, after the reminders had been set up. Results from analyses limited the intention maintenance period were similar to those obtained in the main analyses: there was no evidence for reduced task-positive activation in the offloading conditions. Thus, the results did not support this interpretation.

While the present study provided clear evidence for distinct patterns of activity within task-positive and task-negative networks, there was little evidence for dissociable roles of the regions within these networks. Thus, the foregoing discussion has mostly been focused on distinct networks rather than individual regions. However, previous research has provided evidence for functional distinctions within both task-positive and task-negative networks (Gilbert et al., 2006a, 2012b; Leech et al., 2011); moreover task-positive regions have been fractionated into a “dorsal attention network” (Corbetta & Shulman, 2002) and a “frontoparietal control network” (Spreng et al., 2013; Vincent et al., 2008), which do not necessarily co-activate (Spreng, 2012). Thus it is plausible that individual regions within each network may have played specialized roles in the present paradigm, despite their overall similarity in BOLD signal. Although deactivation of the task-negative network was associated with the requirement to hold representational content about the instructions for a particular trial, this does not necessarily imply that the entire network was involved in this representational function. One possibility might be that a subset of regions is involved in representing relevant content, yielding decreased overall BOLD signal (potentially reflecting an increase in theta-band oscillations; Scheeringa et al., 2008). Seeing as there are strong functional interactions between distinct nodes of this network (Greicius et al., 2003), any reduced BOLD signal in a region involved in representing the content of an intention might then propagate to the other nodes of the network. One region likely to play such a role is medial rostral PFC, which has repeatedly been shown in multivariate decoding studies to carry a representation of the content of delayed intentions (Gilbert, 2011; Momennejad & Haynes, 2012, 2013), and has been suggested to be an anatomical source of frontal midline theta oscillations (Scheeringa et al., 2009; White et al., 2013). This could occur without the other task-negative regions necessarily playing a functional role in the experimental task.

The idea that medial rostral PFC might play a functional role in the present paradigm, accompanied by decreased BOLD signal, is not inconsistent with a role of this region in other tasks (e.g. those involving social cognition) accompanied by increased BOLD signal. One possibility might be that the same neural populations support diverse cognitive demands, sometimes in “theta mode” (accompanied by reduced BOLD signal), and sometimes with greater power in higher frequency bands (accompanied by increased BOLD signal). Another possibility would be that distinct (or partially distinct) populations are engaged by different types of cognitive demand, each population operating with a distinctive spectral profile. This latter possibility would be consistent with evidence that social and nonsocial tasks preferentially yield signal change in nearby but nonidentical regions of medial rostral PFC (Gilbert et al., 2006a, 2007).

While the task-negative response in the present study was defined by a contrast of the no intention condition against the other conditions, other studies have defined task-negative responses using ‘rest’ or fixation baselines in which no cognitive task is explicitly instructed (Shulman et al., 1997). However, even ‘rest’ is an externally imposed task, in the sense that participants are expected to lie still in the scanner, to keep their eyes open or closed as instructed, to refrain from speaking, to await upcoming instructions and so on. Furthermore, similar results have been obtained not only when relatively unconstrained baseline conditions are compared against cognitive tasks, but also when relatively easy task conditions are compared against relatively difficult ones (e.g. Leech et al., 2011). Thus, there is not necessarily any qualitative difference between ‘rest’ or ‘fixation’ conditions, and other low-demand tasks such as the no intention condition of the present study (see Gilbert et al., 2012b, for further discussion).

One unexpected finding in the present study was that task-positive signal, if anything, was *increased* in the conditions involving external reminders. The evidence for this increase was relatively weak, so should be interpreted with caution, but it would be consistent with the recruitment of this network for the process of setting up external reminders and then switching back to the ongoing task, in comparison with

uninterrupted task performance. Furthermore, the task-positive increase with intention offloading was only observed in the 1-target condition; in the 3-target condition the already highly-elevated signal may have masked any additional effect. The requirement for participants to set up reminders themselves in the offloading conditions was included for consistency with the web-based tasks investigated by Gilbert (in press), on which the present paradigm was based. This also ensures that participants must initially encode their intended behavior in a similar manner for trials, rather than being able to rely on a purely perceptual strategy in the offloading conditions, as would be the case if the reminders were automatically provided. However, whereas in the studies reported by Gilbert (in press) participants generally had the option voluntarily to set reminders if they wished, in the present paradigm participants were either instructed that they must set reminders or prevented from doing so. It is therefore an open question which brain regions play a role in the *decision* of whether or not to set an external reminder, presumably related to a metacognitive evaluation of the difficulty of maintaining a purely internal representation and the likelihood of forgetting (see Gilbert, in press; Gilbert, submitted for discussion). Furthermore, it is also unclear whether voluntarily setting an external reminder has a similar influence on brain activity as doing so in response to a mandatory instruction. The present study examined sustained signal change associated with maintaining delayed intentions, rather than transient activity associated with the presentation of cues that drive the execution of those intentions. Thus, the effect of external reminders on such transient processes remains to be examined. For evidence of a transient role of right rostrolateral PFC in triggering shifts from monitoring to cue-directed responses see Howe et al. (2013).

The present research can be seen as investigating ‘distributed cognition’, i.e. the ways in which our cognitive processes can be influenced and in some cases constituted by events that take place outside our brains in the world around us (Clark, 1997, 2010; Hutchins, 1995; Kirsh, 1995), for instance when we ‘outsource’ cognitive control to external artifacts and reminders. This domain has rarely been investigated with neuroimaging techniques, in part due to the restrictions on movement and interaction that they generally impose. However, in order to understand the mechanisms of intelligent, goal-directed behavior, it is important to consider our ability to use the external environment as a means of structuring mental processes and storing representational content, in iterative perception-action cycles (Kirsh, 1995, 1996). The present results provide an example of how our use of the external environment to support performance of a cognitive task – a ubiquitous strategy in everyday life – can alter the underlying brain mechanisms.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.neuroimage.2014.10.021>.

Acknowledgments

JL was supported by an Erasmus scholarship (Deutscher Akademischer Austausch Dienst). SJG is supported by a Royal Society University Research Fellowship.

References

- Andrews-Hanna, J.R., Reidler, J.S., Huang, C., Buckner, R.L., 2010. Evidence for the default network's role in spontaneous cognition. *J. Neurophysiol.* 104 (1), 322–335.
- Antrobus, J.S., 1968. Information theory and stimulus-independent thought. *Br. J. Psychol.* 59 (4), 423–430.
- Barban, F., Carlesimo, G.A., Macaluso, E., Caltagirone, C., Costa, A., 2013. Functional brain activity within the medial and lateral portion of BA10 during a prospective memory task. *Behav. Neurol.* 26 (3), 207–209.
- Barban, F., Carlesimo, G.A., Macaluso, E., Caltagirone, C., Costa, A., 2014. Functional interplay between stimulus-oriented and stimulus-independent attending during a prospective memory task. *Neuropsychologia* 53, 203–212.
- Bird, C.M., Castelli, F., Malik, O., Frith, U., Husain, M., 2004. The impact of extensive medial frontal lobe damage on “theory of mind” and cognition. *Brain* 127, 914–928.
- 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.

- Burgess, P.W., Quayle, A., Frith, C.D., 2001. Brain regions involved in prospective memory as determined by positron emission tomography. *Neuropsychologia* 39 (6), 545–555.
- Burgess, P.W., Scott, S.K., Frith, C.D., 2003. The role of the rostral frontal cortex (area 10) in prospective memory: a lateral versus medial dissociation. *Neuropsychologia* 41 (8), 906–918.
- Burgess, P.W., Dumontheil, I., Gilbert, S.J., 2007. The gateway hypothesis of rostral prefrontal cortex (area 10) function. *Trends Cogn. Sci.* 11 (7), 290–298.
- Burgess, P.W., Gonen-Yaacovi, G., Volle, E., 2011. Functional neuroimaging studies of prospective memory: what have we learnt so far? *Neuropsychologia* 49 (8), 2246–2257.
- Clark, A., 1997. *Being There: Putting Brain, Body, and World Together Again*. MIT Press, Cambridge.
- Clark, A., 2010. *Supersizing the Mind*. Oxford University Press.
- Corbetta, M., Shulman, G.L., 2002. Control of goal-directed and stimulus-driven attention in the brain. *Nat. Rev. Neurosci.* 3, 201–215.
- Duncan, J., 2010. The multiple-demand (MD) system of the primate brain: mental programs for intelligent behaviour. *Trends Cogn. Sci.* 14, 172–179.
- Duncan, J., 2013. The structure of cognition: attentional episodes in mind and brain. *Neuron* 80, 35–50.
- 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, 9673–9678.
- Freedman, D.J., Riesenhuber, M., Poggio, T., Miller, E.K., 2001. Categorical representation of visual stimuli in the primate prefrontal cortex. *Science* 291, 312–316.
- Friston, K.J., Glaser, D.E., Henson, R.N.A., Kiebel, S., Phillips, C., Ashburner, J., 2002. Classical and Bayesian inference in neuroimaging: applications. *NeuroImage* 16, 484–512.
- Gilbert, S.J., 2011. Decoding the content of delayed intentions. *J. Neurosci.* 31, 2888–2894.
- Gilbert, S.J., 2014. Strategic offloading of delayed intentions into the external environment. *Q. J. Exp. Psychol.* <http://dx.doi.org/10.1080/17470218.2014.972963> (in press).
- Gilbert, S.J., 2014. Strategic use of reminders: influence of both domain-general and task-specific metacognitive confidence, independent of objective memory ability, (submitted for publication).
- Gilbert, S.J., Frith, C.D., Burgess, P.W., 2005. Involvement of rostral prefrontal cortex in selection between stimulus-oriented and stimulus-independent thought. *Eur. J. Neurosci.* 21, 1423–1431.
- Gilbert, S.J., Spengler, S., Simons, J.S., Steele, J.D., Lawrie, S.M., Frith, C.D., Burgess, P.W., 2006a. Functional specialization within rostral prefrontal cortex (area 10): a meta-analysis. *J. Cogn. Neurosci.* 18, 932–948.
- Gilbert, S.J., Simons, J.S., Frith, C.D., Burgess, P.W., 2006b. Performance-related activity in medial rostral prefrontal cortex (area 10) during low-demand tasks. *J. Exp. Psychol. Hum. Percept. Perform.* 32, 45–58.
- Gilbert, S.J., Williamson, I.D.M., Dumontheil, I., Simons, J.S., Frith, C.D., Burgess, P.W., 2007. Distinct regions of medial rostral prefrontal cortex supporting social and nonsocial functions. *Soc. Cogn. Affect. Neurosci.* 2, 217–226.
- Gilbert, S.J., Gollwitzer, P.M., Cohen, A.-L., Burgess, P.W., Oettingen, G., 2009. Separable brain systems supporting cued versus self-initiated realization of delayed intentions. *J. Exp. Psychol. Learn. Mem. Cogn.* 35, 905–915.
- Gilbert, S.J., Armbruster, D., Panagiotidi, M., 2012a. Similarity between brain activity at encoding and retrieval predicts successful realization of delayed intentions. *J. Cogn. Neurosci.* 24, 93–105.
- Gilbert, S.J., Bird, G., Frith, C., Burgess, P., 2012b. Does “task difficulty” explain “task-induced deactivation”? *Front. Psychol.* 3, 125.
- Greicius, M.D., Krasnow, B., Reiss, A.L., Menon, V., 2003. Functional connectivity in the resting brain: a network analysis of the default mode hypothesis. *Proc. Natl. Acad. Sci. U. S. A.* 100, 253–258.
- Henseler, I., Krüger, S., Dechent, P., Gruber, O., 2011. A gateway system in rostral PFC? Evidence from biasing attention to perceptual information and internal representations. *NeuroImage* 56, 1666–1676.
- Henson, R., 2007. Efficient experimental design for fMRI. *Statistical Parametric Mapping: The Analysis of Functional Brain Images*, pp. 193–210.
- Howe, W.M., Berry, A.S., Francois, J., Gilmour, G., Carp, J.M., Tricklebank, M., Lustig, C., Sarter, M., 2013. Prefrontal cholinergic mechanisms instigating shifts from monitoring for cues to cue-guided performance: converging electrochemical and fMRI evidence from rats and humans. *J. Neurosci.* 33, 8742–8752.
- Hsieh, L.-T., Ranganath, C., 2014. Frontal midline theta oscillations during working memory maintenance and episodic encoding and retrieval. *NeuroImage* 85, 721–729.
- Hsieh, L.-T., Ekstrom, A.D., Ranganath, C., 2011. Neural oscillations associated with item and temporal order maintenance in working memory. *J. Neurosci.* 31, 10803–10810.
- Hutchins, E., 1995. *Cognition in the Wild*. MIT Press, Cambridge.
- Jensen, O., Lisman, J.E., 1998. An oscillatory short-term memory buffer model can account for data on the Sternberg task. *J. Neurosci.* 18, 10688–10699.
- Kilner, J.M., Mattout, J., Henson, R., Friston, K.J., 2005. Hemodynamic correlates of EEG: a heuristic. *NeuroImage* 28, 280–286.
- Kirsh, D., 1995. The intelligent use of space. *Artif. Intell.* 73, 31–68.
- Kirsh, D., 1996. Adapting the environment instead of oneself. *Adapt. Behav.* 4, 415–452.
- Kriegeskorte, N., Simmons, W.K., Bellgowan, P.S.F., Baker, C.I., 2009. Circular analysis in systems neuroscience: the dangers of double dipping. *Nat. Neurosci.* 12, 535–540.
- Lara, A.H., Wallis, J.D., 2014. Executive control processes underlying multi-item working memory. *Nat. Neurosci.* 17, 876–883.
- Lee, S.-H., Kravitz, D.J., Baker, C.I., 2013. Goal-dependent dissociation of visual and prefrontal cortices during working memory. *Nat. Neurosci.* 16, 997–999.
- Leech, R., Kamourieh, S., Beckmann, C.F., Sharp, D.J., 2011. Fractionating the default mode network: distinct contributions of the ventral and dorsal posterior cingulate cortex to cognitive control. *J. Neurosci.* 31, 3217–3224.
- Lisman, J., Idiart, M., 1995. Storage of 7 +/- 2 short-term memories in oscillatory subcycles. *Science* 267, 1512–1515.
- 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, 393–395.
- McDaniel, M. a., Lamontagne, P., Beck, S.M., Scullin, M.K., Braver, T.S., 2013. Dissociable neural routes to successful prospective memory. *Psychol. Sci.* 24, 1791–1800.
- Michels, L., Bucher, K., Lühinger, R., Klaver, P., Martin, E., Jeanmonod, D., Brandeis, D., 2010. Simultaneous EEG-fMRI during a working memory task: modulations in low and high frequency bands. *PLoS ONE* 5 (4), e10298.
- Momennejad, I., Haynes, J.-D., 2012. Human anterior prefrontal cortex encodes the “what” and “when” of future intentions. *NeuroImage* 61, 139–148.
- Momennejad, I., Haynes, J.-D., 2013. Encoding of prospective tasks in the human prefrontal cortex under varying task loads. *J. Neurosci.* 33, 17342–17349.
- Norman, K. a., Polyn, S.M., Detre, G.J., Haxby, J.V., 2006. Beyond mind-reading: multi-voxel pattern analysis of fMRI data. *Trends Cogn. Sci.* 10, 424–430.
- Okuda, J., Fujii, T., Yamadori, a., Kawashima, R., Tsukiura, T., Fukuda, H., 1998. Participation of the prefrontal cortices in prospective memory: evidence from a PET study in humans. *Neurosci. Lett.* 253 (2), 127–130.
- Phillips, J., Vinck, M., Everling, S., Womelsdorf, T., 2014. A long-range fronto-parietal 5-to 10-Hz network predicts “top-down” controlled guidance in a task-switch paradigm. *Cereb. Cortex* 24, 1996–2008.
- Reynolds, J.R., West, R., Braver, T., 2009. Distinct neural circuits support transient and sustained processes in prospective memory and working memory. *Cereb. Cortex* 19, 1208–1221.
- Scheeringa, R., Bastiaansen, M.C.M., Petersson, K.M., Oostenveld, R., Norris, D.G., Hagoort, P., 2008. Frontal theta EEG activity correlates negatively with the default mode network in resting state. *Int. J. Psychophysiol.* 67, 242–251.
- Scheeringa, R., Petersson, K.M., Oostenveld, R., Norris, D.G., Hagoort, P., Bastiaansen, M.C.M., 2009. Trial-by-trial coupling between EEG and BOLD identifies networks related to alpha and theta EEG power increases during working memory maintenance. *NeuroImage* 44 (3), 1224–1238.
- Shallice, T., Burgess, P.W., 1991. Deficits in strategy application following frontal lobe damage in man. *Brain* 114, 727–741.
- Shulman, G.L., Fiez, J.A., Corbetta, M., Buckner, R.L., Miezin, F.M., Raichle, M.E., Petersen, S.E., 1997. Common blood flow changes across visual tasks. 2: decreases in cerebral cortex. *J. Cogn. Neurosci.* 9, 648–663.
- Simons, J.S., Schölvinck, M.L., Gilbert, S.J., Frith, C.D., Burgess, P.W., 2006. Differential components of prospective memory? Evidence from fMRI. *Neuropsychologia* 44 (8), 1388–1397.
- Spreng, R.N., 2012. The fallacy of a “task-negative” network. *Front. Psychol.* 3, 145.
- Spreng, R.N., Sepulcre, J., Turner, G.R., Stevens, W.D., Schacter, D.L., 2013. Intrinsic architecture underlying the relations among the default, dorsal attention, and frontoparietal control networks of the human brain. *J. Cogn. Neurosci.* 25, 74–86.
- Teasdale, J.D., Dritschel, B.H., Taylor, M.J., Proctor, L., Lloyd, C.A., Nimmo-Smith, I., Baddeley, A.D., 1995. Stimulus-independent thought depends on central executive resources. *Mem. Cogn.* 23, 551–559.
- Uretzky, S., Gilboa, A., 2010. Knowing your lines but missing your cue: rostral prefrontal lesions impair prospective memory cue detection, but not action-intention superiority. *J. Cogn. Neurosci.* 22, 2745–2757.
- Vincent, J.L., Kahn, I., Snyder, A.Z., Raichle, M.E., Buckner, R.L., 2008. Evidence for a frontoparietal control system revealed by intrinsic functional connectivity. *J. Neurophysiol.* 100, 3328–3342.
- White, T.P., Jansen, M., Doegge, K., Mullinger, K.J., Park, S.B., Liddle, E.B., Liddle, P.F., 2013. Theta power during encoding predicts subsequent-memory performance and default mode network deactivation. *Hum. Brain Mapp.* 34 (11), 2929–2943.
- White, S.J., Frith, U., Rellecke, J., Al-Noor, A., Gilbert, S.J., 2014. Autistic adolescents show atypical activation of the brain’s mentalizing system even without a prior history of mentalizing problems. *Neuropsychologia* 56, 17–25.