Hierarchical Cognition causes Task Related Deactivations but not just in Default Mode Regions

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A key aspect of hierarchical cognition is the execution of extended episodes of behavior as one unit. For this entities (e.g. plans, program, schema) that contain elements related to the entire episode are instantiated at the beginning of execution. These subsume and control the subsequent execution of the episode. Because such entities, instantiated at the beginning of execution, prospectively contain elements related to all component steps of the episode, it is plausible that these would dismantle piecemeal as parts of the episode get executed. The load of such entities would therefore be maximum at the beginning of episode execution and decrease gradually as parts of the episode are executed. We found that active load of such entities correlated with deactivation in widespread regions. Across different kinds of task episodes the deactivation was maximum at the beginning, when this load would be maximum. This deactivation then decreased as steps of the episode were executed, returning to baseline at episode completion. This pattern of deactivation was present not just in the default mode regions but in any region not involved in executing the component task items of the episode. Results provide neural evidence of cognitive entities that are related to the execution of extended behavior as one unit. They showed that such entities may underlie the ubiquitous phenomenon task related deactivation, and that this deactivation is shown by all uninvolved regions and is not limited to a fixed set of 'default-mode' regions.

Significance Statement

We prepare breakfasts and write emails and not individually execute their many component acts. Goals are achieved through tasks that correspond to episodes of extended behavior. The current study shows that cognitive entities that enable such hierarchical execution of goal-directed behavior cause the ubiquitously seen deactivation during external task execution. Further, while this deactivation has previously been associated with a defined set of the so called default mode regions, current study demonstrates that deactivation is shown by *any* region not *currently* involved in task execution, including attention related fronto-parietal regions as well as primary sensory and motor regions.

Our goals are typically achieved through task episodes ('preparing breakfast') – periods when cognition is focused on a particular goal and generates a sequence of actions to achieve it. Accounts of hierarchical cognition accept that such task episodes, despite being extended and consisting of a sequence of smaller acts, are executed as *one* task, through cognitive entities (referred to here as programs, but also as plans, schemas, scripts) that are selected and instantiated as one entity but correspond to and control over an extended series of cognitive processes and/or behavioral acts (Miller et al., 1960; Henry and Rogers, 1960; Schank and Abelson, 1977; Cooper and Shallice, 2000). At the beginning of task episodes, a program prospectively related to the entire episode is assembled that would then go on to subsume and control the execution of the sequence of component steps (Schneider & Logan, 2006).

Programs are evidenced by the longer preparation times at the first compared to subsequent steps of task episodes. Hence, whenever a person executes a sequence of motor actions (e.g. typing or reading a word), task lists, or even an episode consisting of unpredictable trials, the first step has the longest RT. This RT is longer before longer or more complex episodes (e.g. more complex action sequences, longer task episodes and task episodes expected to have more frequent task item switches) because programs related to longer/complex episodes take longer to assemble (Rosenbaum et al., 1983. Povel and Collard, 1982; Gordon and Meyer, 1987; Schneider and Logan, 2006; Farooqui and Manly, 2017a).

The subsuming nature of these programs is evidenced by the absence of switch cost across episode boundaries. When task episodes consist of two or more types of task items (e.g. reading or color naming; responding to letters or digits) such that any executed item can repeat or switch from the previous one, the expected switch cost reflected in longer RT for switch trials (Monsell, 2003) is only seen *within* a task episode, and is absent across episode boundaries. The subsuming episode related programs do not allow lower-level task-item related cognitive configurations to interact across episode boundaries because the dismantling of the program at episode completion dismantles

the item related configurations nestled underneath (Lien and Ruthruff, 2004; Schneider and Logan, 2006, 2015).

Programs are also evidenced by the additional widespread activity elicited by episode completions (Farooqui et al., 2012). The intensity and spread of this activity is related to the hierarchical level of the completed episode. Task episode completions elicit greater activity than subtask completions which in turn is greater than sub-subtask completions. Completion of subtasks dismantles programs related to it, leaving the overarching task related programs intact. This elicits less activity than completion of tasks which dismantles programs at all levels.

Further, the above signs of programs are present even when no memorized task sequence is being executed and the knowledge of the identity and sequence of component steps is absent (Farooqui and Manly, 2017a). Neither can the program related pattern of activity elicited at task/subtask completion be explained by invoking changes in working memory representations. Programs, therefore, may not simply be propositional sequence representations in working memory. Instead, they may be better conceived as cognitive structures that ensure that cognitive processing across time remains goal-directed (see discussion).

Here we investigated a key prediction that follows from the execution of task episodes through programs. If programs assembled at the beginning contain elements related to entire length of the episode, then they may dismantle gradually as related parts of the episode get executed, e.g. at the beginning of a task episode made of four steps the program will contain elements related to all four, whereas at step 2, 3 and 4 it will only contain elements related to the remaining three, two and one step - because elements related to earlier steps will have dismantled. The magnitude and the consequent cognitive load of the programs will decrease as the task episode is executed, causing the activity correlated with them to change sequentially along steps 1 to 4.

Across different task episodes we show that beginning of the episode, when the entire program is instantiated, elicited a large deactivation in default mode regions known to deactivate in response to cognitive load. This deactivation gradually decreased as the episode was executed,

reaching baseline towards its completion. Crucially, this pattern of deactivation was not limited to the DMN but was also shown by all other regions that were uninvolved in executing the component steps of the episode.

Results

Experiment 1

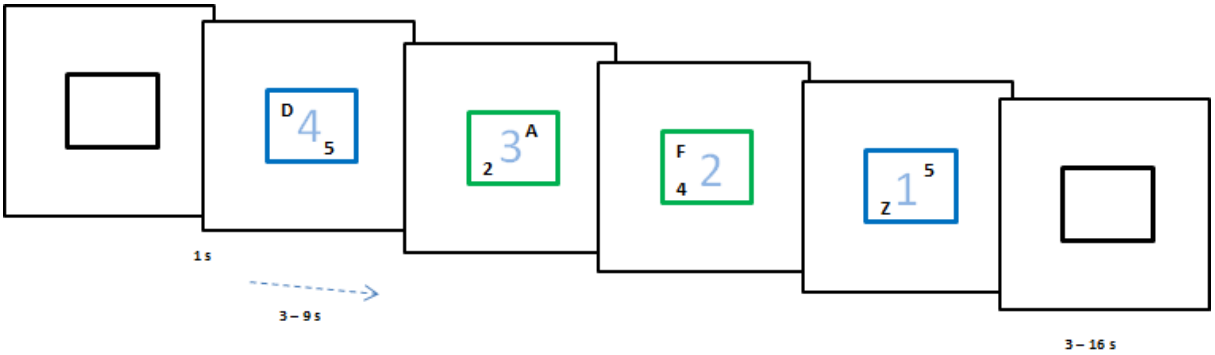

Figure 1. The color of stimulus margin determined if the letter was to be categorized as vowel/consonant (blue) or the number as even/odd (green). Subjects were biased to construe a set of four consecutive trials as *one* task episode. Trials of an episode were preceded and succeeded by black margins and had an irrelevant number in stimulus background that changed 4-3-2-1 across them.

Participants performed a rule-switching task (Monsell, 2003). On each trial a letter and a digit were simultaneously presented for 1 s inside a colored margin. The color of the margin around the stimuli instructed which pre-learned response rule to apply: blue - categorize the letter as a vowel/consonant; green – categorize the digit as even/odd. In both cases they pressed one of the two buttons using index/middle finger of the right hand. Rule was determined at random for each trial.

Crucially, participants were biased toward construing each set of four consecutive trials as one task-episode by a recurring, trial-synchronized 4-3-2-1 background digit countdown that was otherwise irrelevant to the ongoing switching-task. The end of each task-episode was further signaled by the margin turning black.

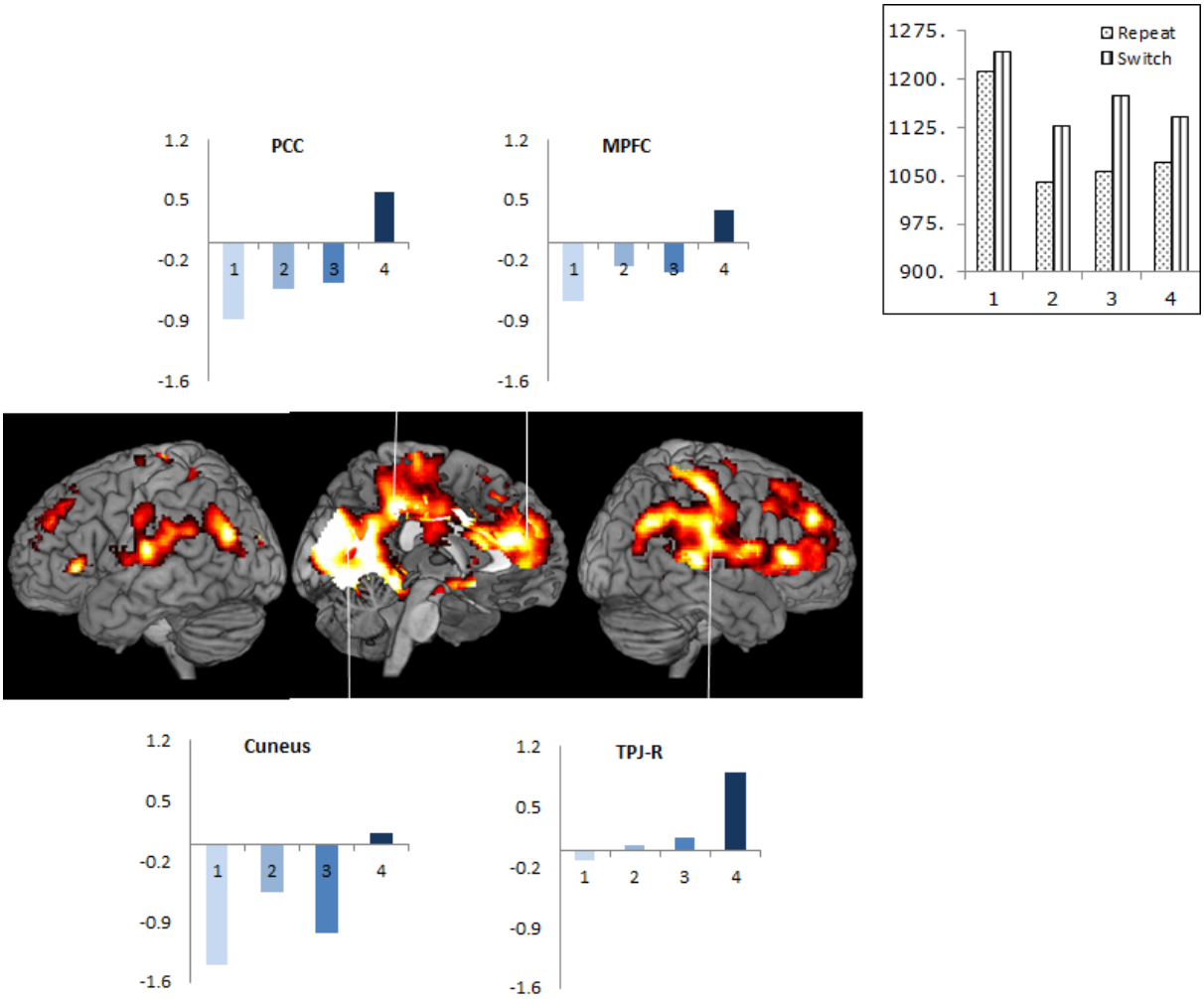

Figure 2. Inset shows reaction times across the four trials of an episode. Note the signs of hierarchical execution: high RT and decreased switch cost at trial 1. Whole brain render shows the regions where activity changed across the four trials - medial occipital regions, cuneus, precuneus, posterior cingulate (PCC), retrosplenial, parahippocampal cortices, temporoparietal junction (TPJ), inferior parietal lobe, right somatosensory and motor regions, medial prefrontal cortex (MPFC), anterior cingulate, right inferior and superior frontal gyri extending onto right anterior prefrontal regions. Linked bar plots show the actual pattern of activity across these trials in regions where whole brain results were particularly strong. Note the sequential change in activity across the four trials.

As expected of task episodes, trial 1 had the longest RT and decreased switch costs ($F_{3,17}$ = 14, $p < 0.001$; inset Figure 2). Figure 2 shows the whole-brain results of regions where activity was different across the four trials of the episode - default mode network (DMN) including medial pre-frontal cortex (MPFC), posterior cingulate (PCC), cuneus, temporoparietal junction (TPJ); right somatosensory and motor cortices; right superior and inferior frontal gyrus. In these regions trial 1 was accompanied by a deactivation and trial 4 with maximal activity, with trials 2 and 3 eliciting intermediate levels of activity.

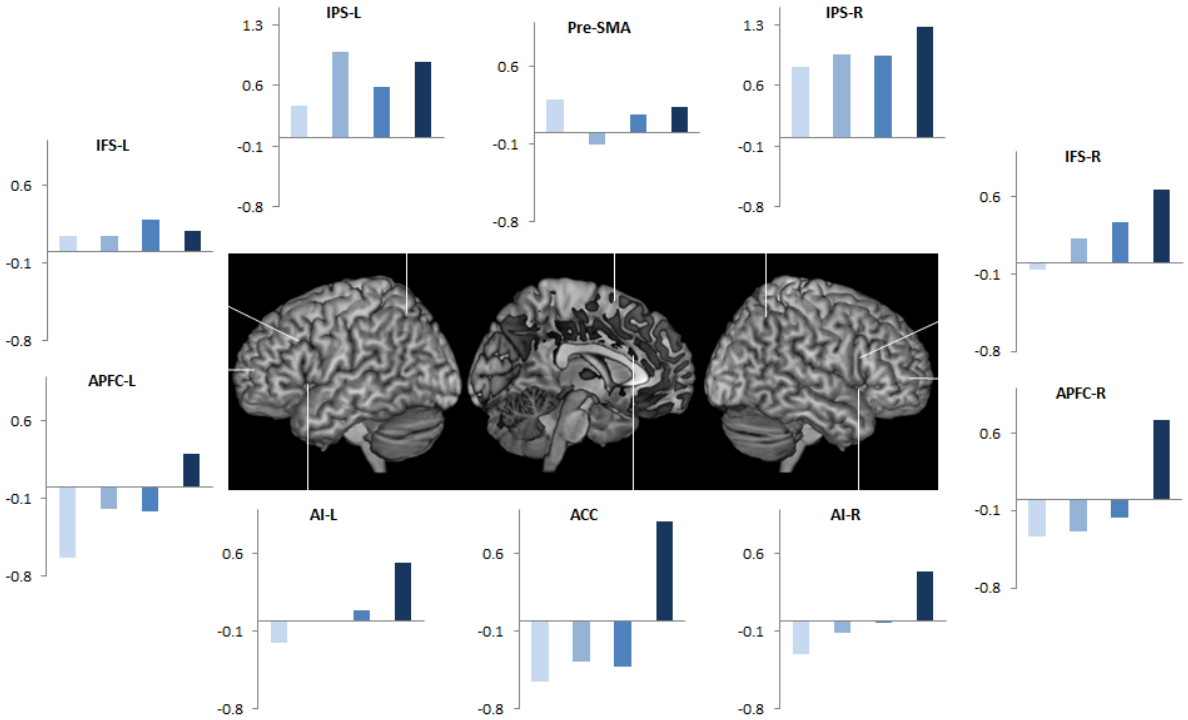

Figure 3. Of the cognitive control related fronto-parietal regions bilateral APFC and ACC showed differential activity across the four trials of the episode similar to that seen in DMN regions (Figure 2). In contrast, IPS, pre-SMA and left IFS showed insignificant change in activity across the four trials. Further, none of the trials elicited deactivations in these regions.

We then conducted a region of interest (ROI) analysis of Multiple Demand (MD) regions - brain areas that are widely observed to be active ("task-positive") across a range of challenging cognitive tasks (Fox et al., 2005; Fedorenko et al., 2013). While these are commonly thought to be anti-correlated to the DMN, we found that some of them – ACC and right APFC ($F_{3,51}>3.1$, $p<0.03$), with strong trends in Left APFC, bilateral insula and right IFS ($p < 0.1$) – showed the same pattern of change in activity across the task episode as the DMN regions (Figure 3). In contrast, other MD regions – left IFS, bilateral IPS and pre-SMA – showed positive and non-differential activity across the four trials.

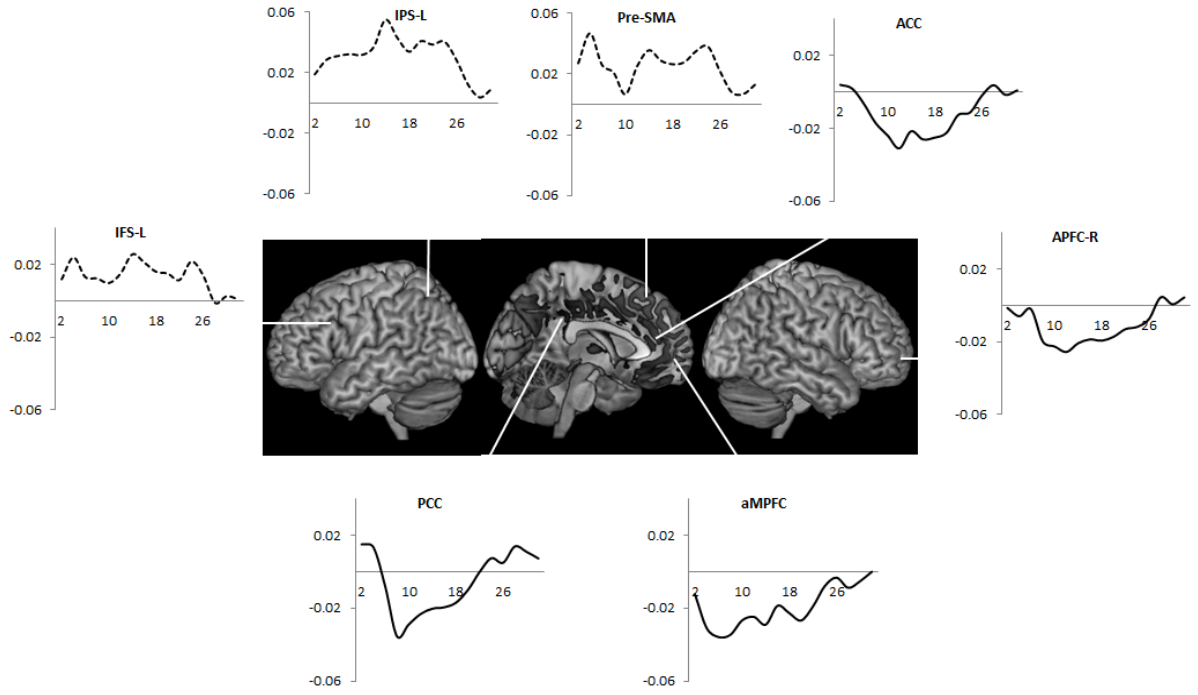

Figure 4. Time course of activity corresponding to the construed task episode in various ROIs. In regions where the four trials elicited differential activity – e.g. PCC, aMPFC, ACC and APFC – beginning of the episode caused a deactivation that returned to baseline across the episode. This is in contrast to fronto-parietal regions that did not show differential activity across the four trials (dotted line graphs). Here the time course did not show any deactivation. x-axis is time (s).

These patterns were also evident in the estimates of time-course of activity across the task episode (Figure 4). DMN ROIs like PCC, aMPFC, and MD ROIs like APFC and ACC showed an initial deactivation starting at the beginning of the episode (i.e. trial 1 onset) followed by gradual return to the baseline as other trials were executed. In contrast, other MD ROIs (left IFS, IPS and pre-SMA) showed a nearly sustained increase in activity.

The above results (e.g. the presence of initial deactivation followed by gradual increase in the DMN regions along with the right motor regions) suggested that the sequential change in activity was preferentially shown by regions not involved in executing individual trials making up the task episode. To investigate this thesis further, we identified regions controlling trial rule switches. These would show higher activity in response to switch trials (i.e. trials where the rule changed from letter to digit or vice versa) compared to repeats. These, shown as hot-spots in Figure 5, included left motor, left IFS, right middle frontal gyrus, pre-SMA extending into ACC, and left IPS. In none of them was activity significantly different across the four trials of the episode ($F_{3, 17} < 1$, $p > 0.3$; see bar graphs in Figure 5). We then identified regions that showed deactivation to task-switches. These (cold-spots Figure 5) were in medial prefrontal regions, posterior cingulate, precuneus, bilateral temporo-parietal junction, right IFS, right premotor and motor regions. From these we arbitrarily selected four clusters adjacent to hot-spots. All of them showed the typical initial deactivation followed by gradual activation across the episode ($F_{3, 17} > 3.8$, $p < 0.02$). The difference across these two groups of ROIs is also evident in the activity time-courses across task-episodes (line plots in Figure 5).

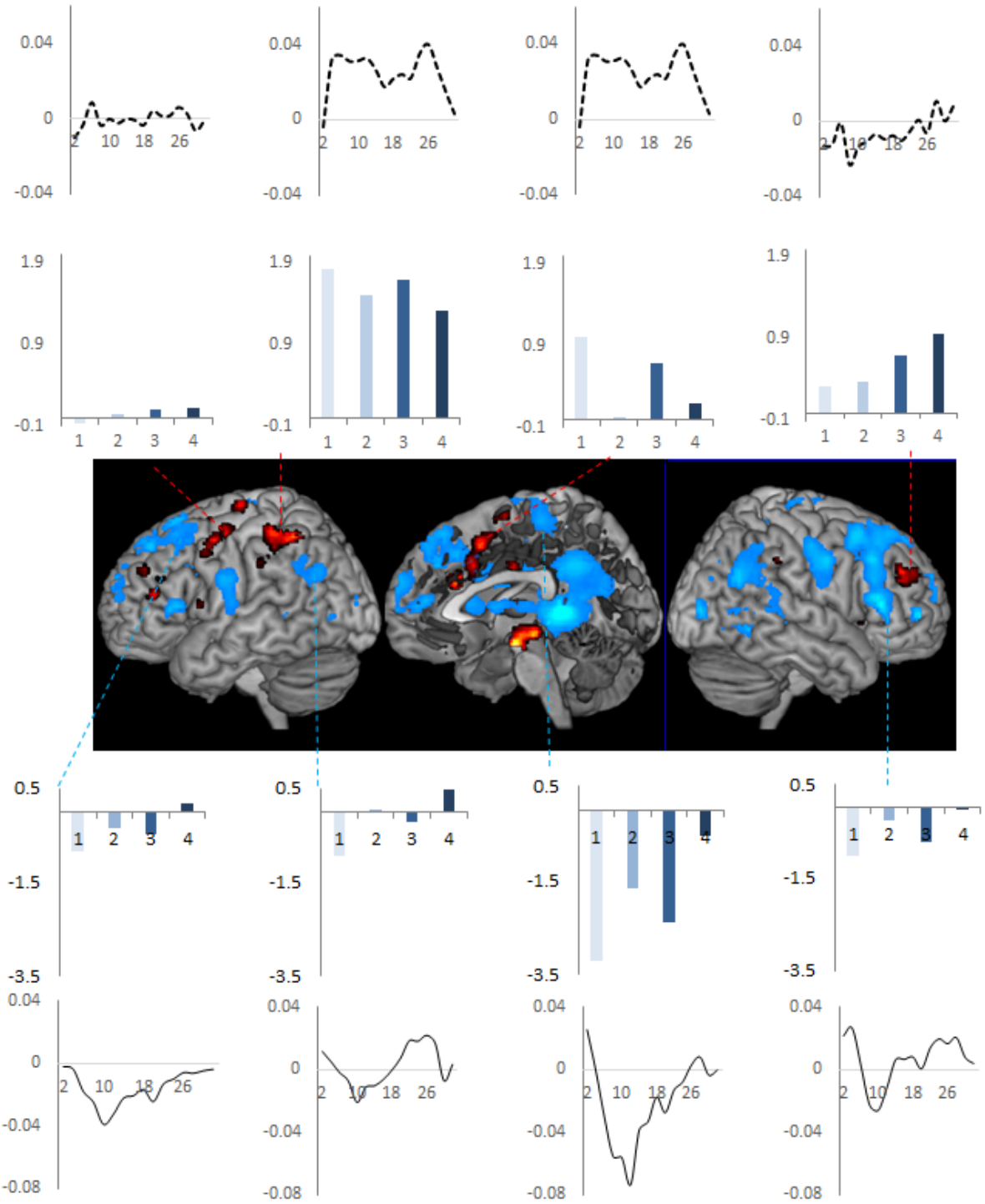

Figure 5. Activity across task episodes in switch trial positive (hot) and switch-trial negative (cold) clusters. Only switch-trial negative clusters showed sequentially changing activity across the task episode. Bar plots show activity across the four trials, line plots show the time course of activity across the task episode.

We next examined activity across task episode in right primary somatosensory and bilateral primary auditory areas, two other regions expected to be unengaged in executing individual trials (trials did not involve any listening nor any action executed through left side of the body). These were contrasted with the left somatosensory hand region (expected to be involved in making right had button press). As shown in Figure 6, the uninvolved regions - bilateral primary auditory and right somatosensory cortices showed task-episode related modulation ($F_{3,51} > 5.0$, $p < 0.02$) while the engaged left somatosensory hand region did not (L vs. R somatosensory difference $F_{3,51} = 9.8$, $p < 0.001$). Again, this showed the presence initial deactivation followed by sequential increase in activity across task episode in regions uninvolved in executing individual component trials.

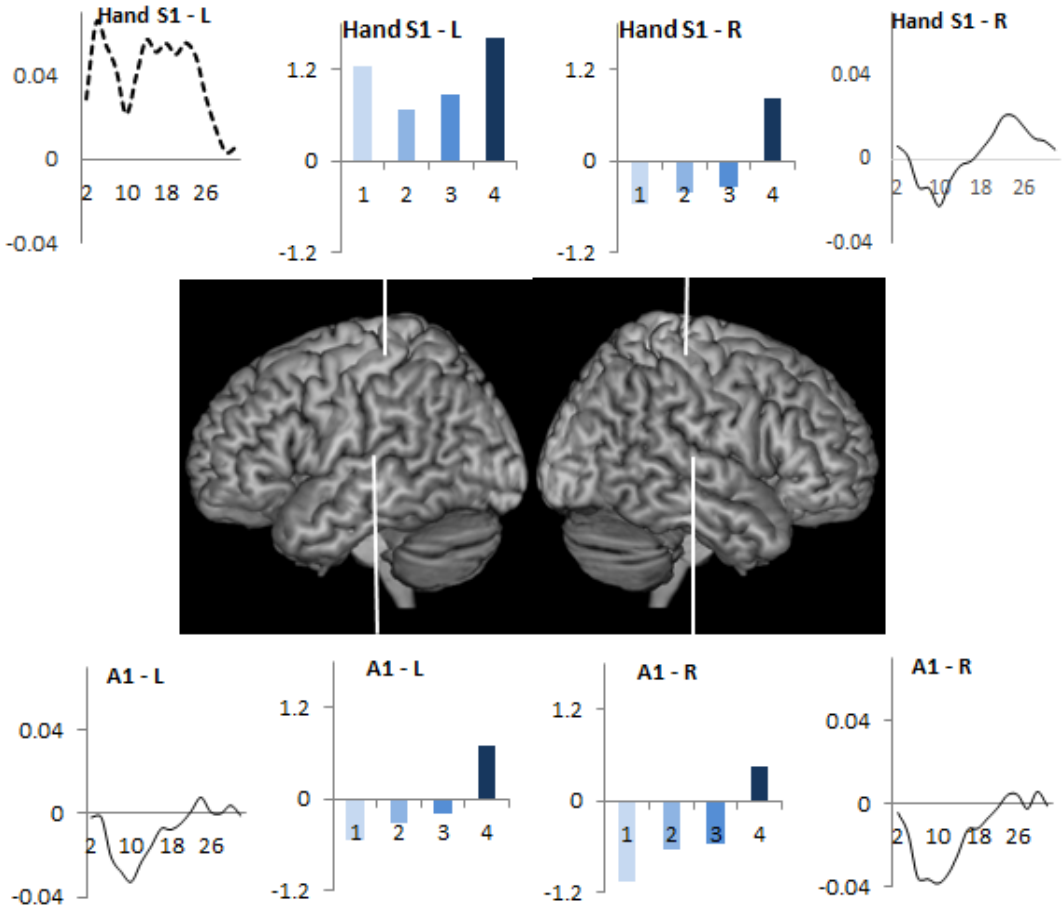

Figure 6. Regions uninvolved in executing individual trials - right somatosensory and bilateral primary auditory cortices (A1) showed a sequential change in activity across the task episode, while the engaged left somatosensory hand region did not.

In summary, when we biased subjects to construe four trials as one task episode, activity in widespread regions changed sequentially across the construed episode. These trials were identical with identical attentional, working memory and control demands. The change in activity across them could not be related to intrinsic features of these trials and suggested that some episode related cognitive entity – the task episode related program – changed as component trials were executed. This sequential change in activity was most evident in regions not involved in executing individual trials - DMN, primary auditory and right somatosensory and motor cortices.

To see the generalizability of these findings, we next investigated a task episode with very different structure and content. Individual steps of a task episode now involved covertly monitoring sequential letter presentations. Since this would be less demanding than executing the rule switch trials of experiment 1, more regions would be *uninvolved* in controlling/executing individual steps, and hence more widespread regions would show sequential increase in activity across the length of the episode.

Experiment 2

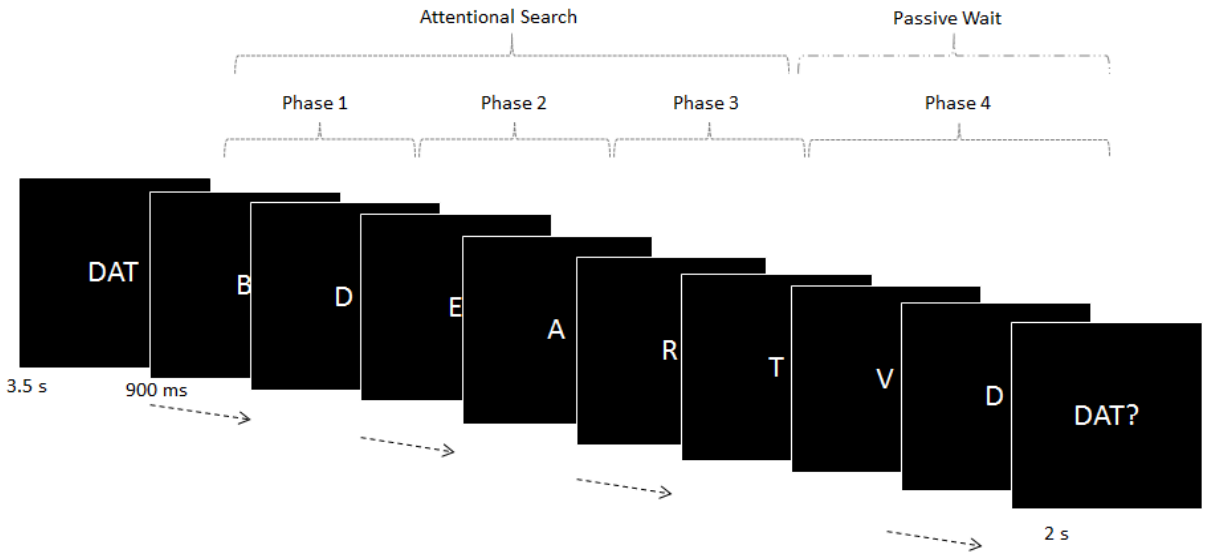

Figure 7. Trial episodes began with a pronounceable three-letter cue. The three letters of this cue were to be covertly detected, in the correct order, in the ensuing letter stream. After all three had been detected, search stopped and subjects waited for the letter stream to end, at which point a probe appeared asking if all three targets had appeared. The trial episode thus consisted four sequential phases – the first three of which involved visual search for a specific letter while the fourth involved a wait for the probe to appear.

At the beginning of a trial episode participants first saw a 3 letter cue (e.g. DAT). They were to then monitor a subsequent sequence of 40 single letters (1 s) for the occurrence of these targets (in the correct order).If the cue was ‘DAT’, searching for A was only relevant once D had been detected and searching for T was only relevant once D and A had been detected. At the end of each sequence participants were probed to report whether or not all three targets had appeared by pressing one of two buttons (right index/middle fingers). A complete set of all three target letters appeared in 50% of trials. Detecting all three targets and answering the probe correctly increased the participant’s score by 1, otherwise the score remained the same. The trial episode thus consisted of four phases (or steps) - three searches plus the passive wait between the third target detection and the probe (Figure 7). The length of these phases varied depending on how many interleaved non-target letters appeared (1 s to 36 s). Task accuracy was high (96.1% ± 2.7).

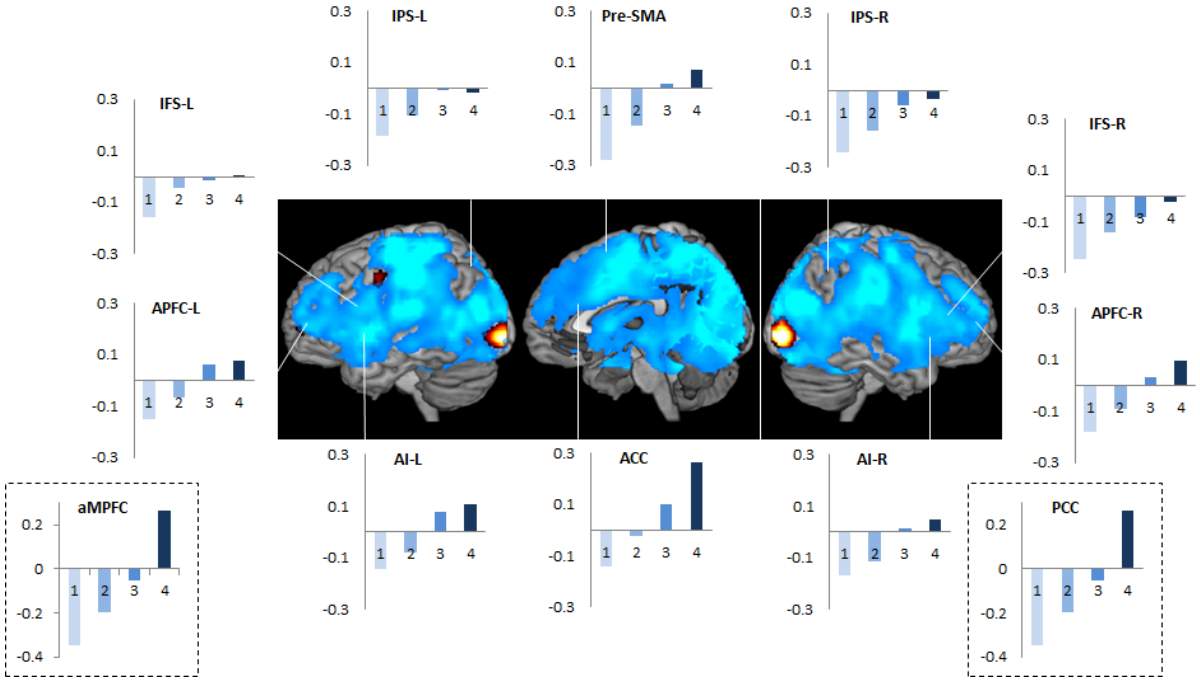

Figure 8. Hot render are the regions where activity increased during attentional search compared to passive rest. Cold render are the regions that showed sequential change in activity across the four phases of the episode. Note that the two renders do not overlap. Very widespread regions (cold render), with the notable exception of some visual regions, showed sequential change in activity across the four phases of the task episode. The pattern of activity (initial deactivation followed by stepwise activation) in all major MD regions was identical to that in the default mode regions (bordered plots).

We first identified areas involved in visual search. Activity in such areas would be higher during visual search (phases 1 to 3) than during the period of passive waiting (phase 4). This was the case in a bilateral cluster that included parts of occipital pole and extended into the inferior division of lateral occipital cortex (Hot regions in Figure 8). Decreasing the threshold to uncorrected $p < 0.05$ showed an additional cluster in left frontal eye field. Other frontal and parietal regions did not show any significant cluster. In the light of experiment 1, remaining cortical regions can be expected to show change in activity across the length of the episode.

Cold regions in Figure 8 show regions where activity increased across the sequential phases making up the trial episode. This pattern was present in very widespread regions that included all major DMN and MD regions as well as all non-visual sensory and motor cortices. Parts of cerebellum, basal ganglia, thalamus and medial temporal regions also showed an identical pattern. Thus, almost the entire brain with some islands of exception (including notably, middle occipital regions that were sensitive to visual search) showed sequential change in activity across the length of the trial episode.

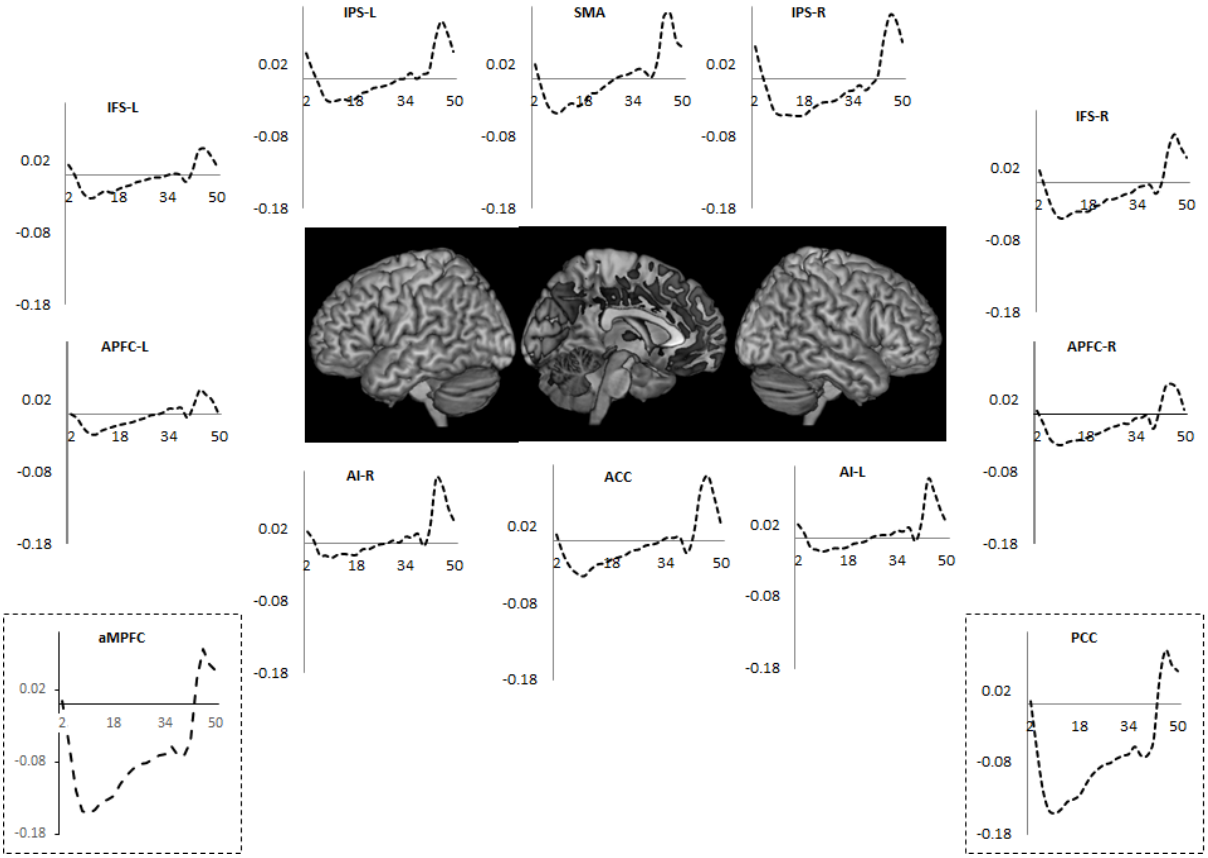

Figure 9. Time-course of activity across the task episode in various control related fronto-parietal regions. Note that the pattern was identical to that in a representative DMN regions (PCC). Across all of them, the beginning of the episode elicited a deactivation that gradually decreased across the length of the episode, with episode completion (at 40 s) eliciting a strong activation.

The time-course of activity corresponding to the trial episode was similar to experiment 1 (Figure 9). All MD and DMN ROIs showed the same pattern - initial deactivation followed by gradual return to the baseline across the duration of the episode. Thus, despite the different structure and content of task episodes, experiment 2 showed the same pattern of sequentially changing activity as experiment 1. Greater presence of this activity in MD and sensory (except visual) and motor regions further supported the thesis that such activity is shown by regions uninvolved in executing component task items. In experiment 3 we directly tested this thesis by alternating hand-of-response across different task-episodes.

Experiment 3

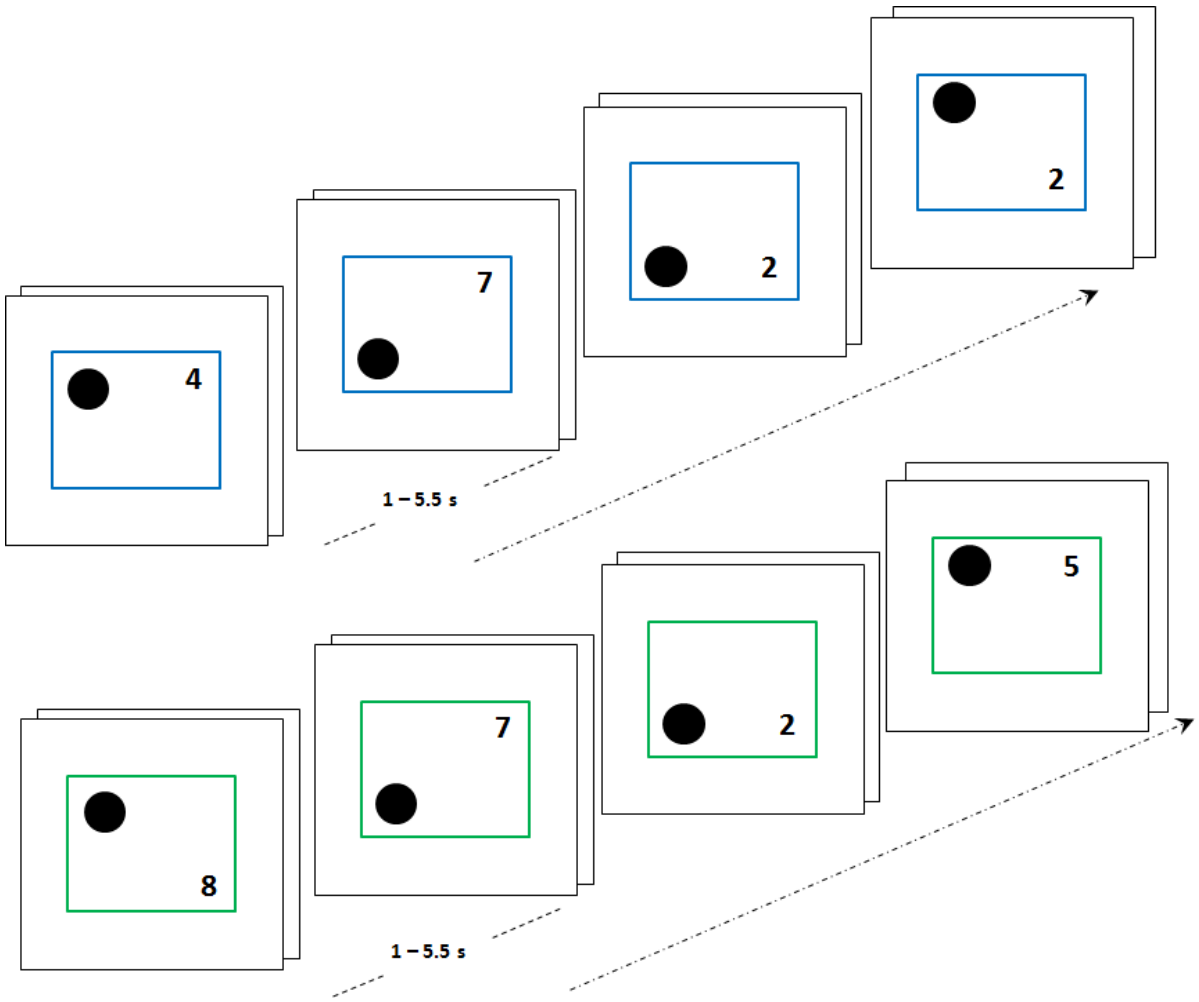

Figure 10. Episodes consisted of four phases, each of which involved a pair of trials i.e. two trials that followed without any interval. In a shape episode (blue margin trials) participants categorized the shape as above/below the center with their left hand, while in a number episode (green margin trials) they categorized the number as odd/even with their right hand.

Participants executed two kinds of task episodes – Number and Shape (Figure 10). The identity of the episode was cued by the color of stimulus margins (e.g. Number: Green, Shape: Blue). In both they executed a four phase trial episode. Each phase consisted of a pair of trials i.e. two trials juxtaposed without any interval. On every trial of number episodes participants indicated if the displayed number was even or odd using their right hand (index finger: even, middle finger: odd). During shape episodes participants indicated if the black circle in the stimuli was above or below the center using their left hand (middle finger: up, index finger: down). Additionally, participants kept an internal count and after executing 4 phases (or 8 trials) pressed an extra button with the middle finger of their task relevant hand, i.e. left hand during shape episodes, right hand during number episodes.

Through a separate localizer task block we delineated somatosensory and motor voxels that were more active during right and left hand button presses. These can be expected to be engaged in executing individual trials of number and shape episodes. If the deactivation followed by increase in activity across the task episode is shown by regions not involved in executing component task items then during the number episodes this pattern will be shown by the left hand related voxels lying in the right hemisphere, and during shape episodes by the right hand related voxels lying in the left hemisphere. Regions like PCC and MPFC (a DMN region) and primary auditory cortices (part of the uninvolved sensory regions) will show this behavior during both task episodes.

The first trial of episodes had the highest RT (1.7 vs 0.8 sec; $p < 0.001$). Accuracy averaged 97.5 %.

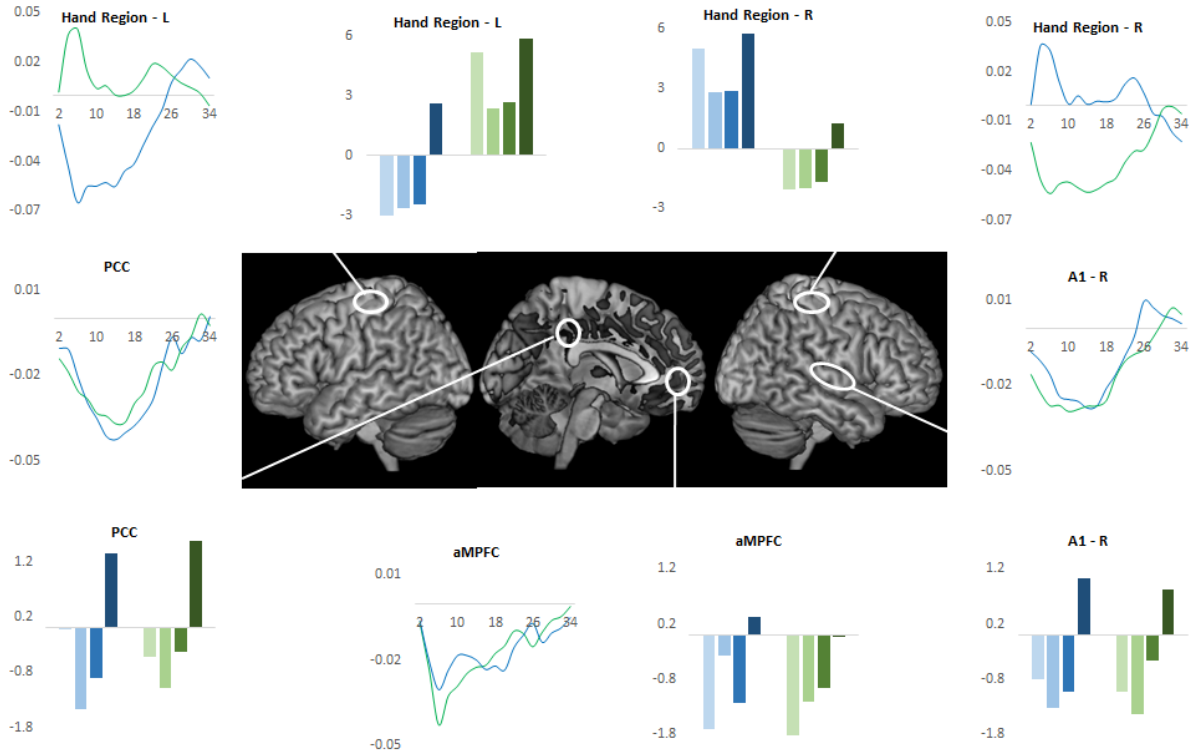

Figure 11. During the right hand executed number episode activity in the uninvolved left hand related right somatosensory and motor region showed initial deactivation followed by gradual increase. During the left hand executed shape episode this same pattern was shown by the right hand related left somatosensory and motor region. DMN regions – PCC and aMPFC and primary auditory cortex showed this pattern during both task episodes.

As apparent in Figure 11, the hand sensory-motor region in left hemisphere controlling the right hand showed initial decrease followed by stepwise increase during the left hand executed shape episodes. In contrast, the hand sensory-motor region in right hemisphere controlling the left hand showed initial decrease followed by stepwise increase during the right hand executed number episodes. Regions like PCC and aMPFC (DMN regions) and primary auditory cortex (an uninvolved sensory region) showed this pattern during both episodes.

General Discussion

In three different experiments with task episodes differing in length, structure and content, activity in widespread regions showed a deactivation with episode beginning followed by gradual return to the baseline across the length of the episode. This change in activity cannot be accounted for by any characteristic of component steps because these steps were identical in their intrinsic demands. Instead, it suggested a gradual change in some episode related cognitive entity as parts of the task episode were executed. We suggest that this entity was the task episode related program – cognitive structures that embodied the set of higher level commands through which the corresponding episode of cognition and behavior was controlled and executed across time as one unit.

Such programs are created at the beginning of task episodes and manifest in the characteristic behavior seen at step 1 of task sequence executions (Rosenbaum et al., n.d.; Schneider and Logan, 2006; Farooqui and Manly, 2017a), and are dismantled at task episode completions eliciting characteristically widespread activity (Fujii and Graybiel, 2003; Farooqui et al., 2012; Crittenden et al., 2015; Simony et al., 2016). The current experiments suggested that instantiation of these programs may be correlated with the initial widespread deactivation, and the subsequent decrease in this deactivation may be related to the piecemeal dismantling of the program as related parts of the episode get executed and the 'load' of the active program decreases. While the current and related studies have evidenced the existence of programs, they do not tell much about their nature and content.

Task Episode related Programs

Past accounts have emphasized the ability of programs to explicitly specify the identity and sequence of component behavioral steps (Miller et al., n.d.; Schank and Abelson, 1977; Cooper and Shallice, 2000). However, this function of programs cannot be fulfilled in task episodes where

identity and sequence of behavioral steps were not known e.g. experiment 1. Even in task episodes where the identity and sequence of component steps were known, key observations suggested that a program is not merely a working memory representation of component steps. In experiment 2 participants had a cue in working memory (e.g. 'DAT). It is unlikely that parts of this cue representation was removed from working memory after the first search. After all what was likely to have been maintained in memory was the conglomerate representation 'DAT' and not D, A and T individually. Hence, even here change in activity cannot be related to a change in task step representations being maintained in working memory. In our view the program may have to do a lot of other functions beyond being a repository of representations of component acts and hence it may have of lot of other components. What follow are some possibilities.

Perhaps, the program may be a means of organizing cognition across time into task focused cognitive episodes. Through it various ongoing irrelevant processes and representations are cleared out from a position where they can compete for cognitive reserves (or disrupt task execution) and maintained in abeyance across time. At the same time, various task relevant learnings, memories, skills, dispositions, knowledge and expectancies, and the corresponding configurational changes in various perceptual, attentional, mnemonic, and motor processes are brought to fore (Miller et al., n.d.; Bartlett and Bartlett, 1932; Rogers and Monsell, 1995; Mayr and Kliegl, 2000; Logan and Gordon, 2001). Programs could have embodied the entire set of commands that will bring about such changes in various cognitive domains automatically across time, such that at each point of the task episode the cognition is in the most goal-directed state achievable with available task knowledge.

In task episodes of experiment 1 amongst other things, processing related to mind-wandering, ongoing unconscious goals, task irrelevant sensory and motor processing etc. had to be relegated. Likewise, the predictiveness of the episode utilized to make anticipatory changes, e.g. knowledge that responses were right handed, visual attention limited to area around fixation, along with an implicit idea of inter-trial intervals, could have been used to increase relevant

preparativeness at times when a stimulus was expected and decreased otherwise. Furthermore, the entire sequence of such anticipatory changes could have been sequentially organized according to the knowledge that four trials were to be executed to complete the episode.

Importantly, such changes are brought about with the intent of achieving a goal. Hence the cognitive structures bringing about these changes is likely to be linked to goal. Rather than seeing goals as merely end states to be achieved, goals may be better conceived as cognitive structures or programs geared towards reaching that end state. Indeed a wide variety of frameworks accept that goals are important for the control and execution of tasks that lead to their achievement (James, 1890; Lewin, 1926; Greenwald, 1972; Prinz, 1987; Jeannerod, 1988; Meyer and Kieras, 1997; Gollwitzer and Sheeran, 2006; Anderson, 2014). For this to happen goals have to correspond to some cognitive entity that is active during the task episode (James, 1890; Kruglanski and Kopetz, 2009). The program evidenced here may be the means of rapidly achieving the widespread goal directed changes across time.

Relatedly, these programs may also be seen as the means of instantiating attention and other forms of cognitive control across time. It is well known that attention cannot be sustained indefinitely (Manly et al., 1999). Faced with an episodic task, cognition may instantiate attention in chunks that last for a time period and have to be re-instantiated. The instantiation of these chunks may be synced with conceived task boundaries. Hence, an attentional chunk may be instantiated at a beginning of a task-episode. The ‘magnitude’ instantiated may be such that it lasts the estimated duration of the episode.

The deactivation may either be a result of the configuration of neural activities of a region to maintain program related structures, or be an effect of the ‘load’ of the program being maintained in a different region, or perhaps both. In any case, task episodes may be a neurally global phenomenon that involve nearly the entire cortex, either as activations for executing the component items making up the episode or as part of the program related deactivation (Gonzalez-Castillo et al., 2012).

Critical questions remain - Why did the beginning of episodes (and hence assembly of programs) elicit a deactivation and not an activation? How were these programs assembled?

Program Related Deactivation

The initial large deactivation followed by stepwise decrease in it was shown by a variable set of regions that was not involved in executing individual task items/steps of the episode. When in experiment 1 the episode consisted of rule switching trials executed with the right hand sequential change was shown, amongst others, by the regions associated with DMN, right somatosensory and motor regions, and primary auditory cortices. In experiment 2 the task content of the episode was simpler - covert monitoring of easily visible letter sequences - and did not involve any motor response. Now the same pattern was additionally shown by all MD as well as sensory (except visual) and motor regions. Experiment 3 showed that during task episodes executed with the right hand such activity was in right somatosensory and motor cortices while during left hand executed episodes in left somatosensory and motor cortices.

Deactivations are ubiquitously seen during external task executions and have been attributed to the shutting down of the network involved in internal cognition (e.g. mind wandering or self-referential processing) during periods of external attention and/or working memory (Ingvar, 1979; Shulman et al., 1997; Raichle et al., 2001; Fox et al., 2005). We show that such deactivations decrease as parts of the construed episode are executed, even when sequential parts of the episode were identical in terms of external attention and the amount of propositional task information being maintained in working memory. We propose that programs may be the primary cause of task related deactivations. Association of such deactivations with external attention and working memory seen in past (e.g. (Shulman et al., 1997; Greicius et al., 2003) may have been a result of the fact that sustaining attention and maintaining task relevant information across time (working memory) always occur in the context of some form of extended task episode, and may themselves

be instantiated through programs.

Program Related Deactivation is Not Limited to the DMN

This study showed that deactivation during task episodes can occur in any brain region that is not currently involved in controlling or processing the task content of the steps making up the episode, and is not limited to a fixed set of specialized regions. Hence across experiments this was also shown by sensory and motor cortices, and even the MD regions. The primary cause of task related deactivation was therefore not the defaultness of deactivated brain regions or their preference for internal cognition or mind wandering (Mason et al., 2007; Spreng et al., 2009). Although these may be the functions of some deactivated regions.

Previously, somatosensory, motor, auditory and visual regions have been seen to deactivate during task situations when they were not involved (Allison et al., 2000; Nirkko et al., 2001; Merabet et al., 2006; Hairston et al., 2008; Linke et al., 2011; Farooqui and Manly, 2017b). The current results suggest that such deactivations may be related to the larger phenomenon of task related deactivation traditionally characterized with reference to the DMN. These results also argue against a necessary anti-correlation between the MD and DMN regions (c.f. 23). Of the MD regions some in experiment 1 and all in experiment 2 showed identical patterns of deactivation as the DMN regions.

In summary, whenever cognition/behavior is parsed into task episodes a number of brain regions deactivate at the beginning and then show sequential increase as parts of the episode are executed, suggesting the presence of episode related programs that are assembled at the beginning and dismantle piecemeal with as parts of the episode are executed. These results make three key suggestions related to task related deactivations: (1) Programs may be the cause of these deactivations. (2) These deactivations may not be limited to DMN purported to specialize in internal cognition and or mind wandering, but may be shown by any region not currently involved in executing individual components of the task episode. (3) DMN and MD regions may not be

specialized to anti-correlate during task executions; instead, depending on the nature of the task episode, they may show identical patterns of deactivation.

Methods

Experiment 1

Inter trial interval varied between 3 to 9 (average 5.5) s. The interval between two trials across the episode boundary (i.e. the fourth and the first trial) was longer and varied from 3 to 16 (average 8) s. Participants did a total of 100 trials or 25 trial episodes. All stimuli were presented at the center of the screen, visible from the participant's position in the scanner via a mirror mounted within the head coil. The square in which the letter and the number appeared subtended a visual angle of around 2.5°. The letter and number were presented in Arial font (size 30) and could appear at any of the corners of the outer square. Other than the 4-trial episodes described here, the experiment also involved 8 trial episodes. However, their analysis presents a further detail of the phenomenon described here which we deal with in another upcoming paper (Farooqui & Manly, in preparation).

Experiment 2

All stimuli were presented at the center of the screen, visible from the participant's position in the scanner via a mirror mounted within the head coil. Letters subtended a visual angle of 2° vertically. The experiment was controlled by a program written in Visual Basic. Participants learnt the task in a 10 min prescan practice session. The scanning session lasted an hour and was divided into three separate runs, each consisting of 14 trials.

Experiment 3

Stimuli consisted of a circle and a number on the left and right sides respectively of a surrounding square. The color of the outer square was green or blue respectively during number and

shape episodes. Stimuli remained on screen till a response was made. An episode consisted of eight trials grouped in pairs. Hence there was no inter-trial interval between trials 1 & 2, 3 & 4, 5 & 6, and 7 & 8. Participants were instructed that the episode consisted of 4 phases, with each phase consisting of 2 trials. They were to keep a covert count of the number of phases they had executed and were to press their response button twice at the end of the fourth phase (i.e. 8th trial). The interval between consecutive phases was jittered from 1 to 7 s. The surrounding square remained on for the entire duration of the episode and went off at its completion. The interval between successive episodes was jittered between 1 and 7 s. Participants executed a total of 30 task episodes, that consisted of equal number of shape and number episodes. The two episode types were randomly interspersed.

Localizer Session: After the main session in experiment 3, participants executed a 10 minute localizer task. This consisted of 16 second long alternating blocks of face and place trials. On face trials they categorized face pictures as male or female; on place trials they categorized scenes as indoor or outdoor. Importantly, for one block type they used index and middle finger of right hand and for the other same fingers of left hand. The actual combination was balanced across participants.

Participants

Eighteen (11 females; mean age, 25 ± 4.1years), twenty one (15 females; mean age, 24.5 ± 4.1years) and seventeen (14 females; mean age 24.2 ± 5.3 years) participants were recruited in experiments 1 to 3 respectively from the Medical Research Council and Cognition and Brain Sciences Unit (Cambridge, UK) volunteer panel. All were right handed and had normal or corrected vision. Informed consent was taken, and the participants were reimbursed for their time. The study

had the approval of Hertfordshire Local Research Ethics Committee.

Acquisition

fMRI data were acquired using a Siemens 3T Tim Trio scanner with a 12 channel head coil. A sequential descending T2*-weighted echo planar imaging (EPI) acquisition sequence was used with the following parameters: acquisition time, 2000 ms; echo time, 30 ms; 32 oblique slices with slice thickness of 3 mm and a 0.75 mm interslice gap; in-plane resolution, 3.0 × 3.0 mm; matrix, 64 × 64; field of view, 192 mm; flip angle, 78°. T1-weighted MP RAGE structural images were also acquired for all participants (slice thickness, 1.0 mm; resolution, 1.0 × 1.0× 1.5 mm; field of view, 256 mm; 160 slices). Experimental tasks started after 10 dummy scans had been acquired. These were discarded from the general linear model to allow for T1 equilibration effects.

Analysis

The fMRI data were analyzed using SPM8 (experiments 1 and 2) and SPM12 (experiments 3) using the automatic analysis pipeline (Cusack et al., 2015). Before statistical analysis, all EPI volumes were slice-time corrected using the first slice as a reference and then realigned into a standard orientation using the first volume as a reference. These realigned volumes were then normalized into the Montreal Neurological Institute (MNI) space and spatially smoothed using an 8 mm full-width half-maximum Gaussian kernel. During the normalization stage, voxels were resampled to a size of 3 × 3 × 3 mm. The time course of each voxel was high pass filtered with a cutoff period of 90 s. Statistical analysis was carried out using general linear models (GLMs).

In experiment 1, individual trials occurring at step positions 1 to 4 were modeled with separate event regressors of 1 s duration. In experiment 2, the three target events (data not presented in current paper) were modelled with event regressors of no duration while the four phases along

with the cue and probe were modelled using epoch regressors of width equal to their durations. In experiment 3 each paired-trial was modelled with an epoch regressor that extended from the stimulus onset for the first trial of the pair up till the response to the second trial. In localizer session of experiment 3 face and place trial blocks were modelled with epoch regressors equal to their length.

Across all experiments movement parameters and block means were included as covariates of no interest. Regressors were convolved with a basis function representing the canonical hemodynamic response (HRF). Parameter estimates for each regressor were calculated from the least-squares fit of the model to the data, and estimates for individual participants were entered into a random effects group analysis.

Whole-brain comparisons in experiment 1 were performed using analysis of variance across the estimates of activity from sequential trials or phases. In experiment 2 we did a direct contrast that looked for higher activity in phases 3 and 4 compared to 1 and 2. Unless otherwise specified, all results are reported at a threshold of $p < 0.05$ and corrected for multiple comparisons using the false discovery rate. Coordinates for peak activation are reported using an MNI template.

To derive the time course of activity across entire task episodes, we modelled 32, 52 and 34 seconds of activity in experiments 1, 2 and 3, respectively, following the beginning of the episode with 16, 26 and 17 finite impulse regressors. The experiment 2 analysis additionally had cue, probe and target events modelled as epoch regressors of width equal to their durations and convolved with HRF.

To capture the frontoparietal regions seen to be engaged by a wide variety of task demands as well as the default mode regions known to deactivate across them regions of interest (ROIs) were created as spheres of 10 mm radius at coordinates that have been shown to be consistently activated or deactivated in varied tasks (Dosenbach et al., 2006; Duncan, 2006). The ROIs (in MNI space) were bilateral inferior frontal sulcus (IFS; central coordinate ±41 23 29), bilateral intraparietal

sulcus (IPS; ± 37 56 41), bilateral anterior insula extending into frontal operculum (AI/FO; ± 35 18 3), anterior cingulate cortex (ACC; 0 31 24), and presupplementary motor area (pre-SMA; 0 18 50), all taken from (Duncan, 2006); bilateral anterior prefrontal cortex ROIs (APFC; 27 50 23 and ±28 51 15) were taken from (Dosenbach et al., 2006); posterior cingulate cortex (PCC; -8 -56 26) and Anterior Medial Prefrontal cortex (aMPFC; -6 52 -2) were taken from (Andrews-Hanna et al., 2010). Coordinates for hand primary somatosensory area used in Experiment 1 were taken from Pleger et al. (2009). Primary auditory cortex ROI was made using probabilistic maps in the anatomy toolbox of SPM 8. ROIs were constructed using the MarsBaR toolbox for SPM (http://marsbar.sourceforge.net). Estimated data were averaged across voxels within each ROI using the MarsBaR toolbox, and the mean values were exported for analysis using SPSS.

References

Allison JD, Meador KJ, Loring DW, Figueroa RE, Wright JC (2000) Functional MRI cerebral activation and deactivation during finger movement. Neurology 54:135–142 Available at: http://www.ncbi.nlm.nih.gov/pubmed/10636139 [Accessed January 26, 2017].

Anderson JR (2014) Rules of the Mind. Taylor & Francis. Available at: https://books.google.com/books?id=KjyZAgAAQBAJ&pgis=1 [Accessed September 13, 2015].

Anderson JR, Bothell D, Lebiere C, Matessa M (1998) An Integrated Theory of List Memory. J Mem Lang 38:341–380 Available at: http://www.sciencedirect.com/science/article/pii/S0749596X97925535 [Accessed March 14, 2014].

Andrews-Hanna JR, Reidler JS, Sepulcre J, Poulin R, Buckner RL (2010) Functional-anatomic

fractionation of the brain's default network. Neuron 65:550–562 Available at: http://www.ncbi.nlm.nih.gov/pubmed/20188659 [Accessed October 26, 2017].

Bartlett SFC, Bartlett FC (1932) Remembering: A Study in Experimental and Social Psychology. Cambridge University Press. Available at: https://books.google.com/books?hl=en&lr=&id=WG5ZcHGTrm4C&pgis=1 [Accessed September 13, 2015].

Cooper R, Shallice T (2000) CONTENTION SCHEDULING AND THE CONTROL OF ROUTINE ACTIVITIES. Cogn Neuropsychol 17:297–338 Available at: http://www.ncbi.nlm.nih.gov/pubmed/20945185 [Accessed October 26, 2017].

Crittenden BM et al. (2015) Recruitment of the default mode network during a demanding act of executive control. Elife 4:e06481 Available at: http://www.ncbi.nlm.nih.gov/pubmed/25866927 [Accessed January 10, 2017].

Cusack R, Vicente-Grabovetsky A, Mitchell DJ, Wild CJ, Auer T, Linke AC, Peelle JE (2015) Automatic analysis (aa): efficient neuroimaging workflows and parallel processing using Matlab and XML. Front Neuroinform 8:90 Available at: http://journal.frontiersin.org/article/10.3389/fninf.2014.00090/abstract [Accessed January 27, 2017].

Dosenbach NUF, Visscher KM, Palmer ED, Miezin FM, Wenger KK, Kang HC, Burgund ED, Grimes AL, Schlaggar BL, Petersen SE (2006) A core system for the implementation of task sets. Neuron 50:799–812 Available at: http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3621133&tool=pmcentrez&rendertype=abstract [Accessed June 2, 2015].

Duncan J (2006) EPS Mid-Career Award 2004: Brain mechanisms of attention. Q J Exp Psychol 59:2–27 Available at: http://www.tandfonline.com/doi/abs/10.1080/17470210500260674

[Accessed October 22, 2015].

Farooqui AA, Manly T (2017a) Cognitive Entities Underpinning Task Episodes. bioRxiv:216796 Available at: https://www.biorxiv.org/content/early/2017/11/09/216796 [Accessed December 4, 2017].

Farooqui AA, Manly T (2017b) When attended and conscious perception deactivates fronto-parietal regions. Cortex Available at: http://www.sciencedirect.com/science/article/pii/S001094521730299X [Accessed October 24, 2017].

Farooqui AA, Mitchell D, Thompson R, Duncan J (2012) Hierarchical organization of cognition reflected in distributed frontoparietal activity. J Neurosci 32:17373–17381 Available at: http://www.jneurosci.org/content/32/48/17373.short [Accessed June 1, 2015].

Fedorenko E, Duncan J, Kanwisher N (2013) Broad domain generality in focal regions of frontal and parietal cortex. Proc Natl Acad Sci U S A 110:16616–16621 Available at: http://www.pnas.org/content/110/41/16616.short [Accessed May 8, 2015].

Fox MD, Snyder AZ, Vincent JL, Corbetta M, Van Essen DC, Raichle ME (2005) The human brain is intrinsically organized into dynamic, anticorrelated functional networks. Proc Natl Acad Sci U S A 102:9673–9678 Available at: http://www.ncbi.nlm.nih.gov/pubmed/15976020 [Accessed February 4, 2017].

Fujii N, Graybiel AM (2003) Representation of Action Sequence Boundaries by Macaque Prefrontal Cortical Neurons. Science (80-) 301:1246–1249 Available at: http://www.ncbi.nlm.nih.gov/pubmed/12947203 [Accessed February 4, 2017].

Gollwitzer PM, Sheeran P (2006) Implementation Intentions and Goal Achievement: A Meta-analysis of Effects and Processes. Adv Exp Soc Psychol 38:69–119.

Gonzalez-Castillo J, Saad ZS, Handwerker DA, Inati SJ, Brenowitz N, Bandettini PA (2012) Whole-brain, time-locked activation with simple tasks revealed using massive averaging and model-free analysis. Proc Natl Acad Sci U S A 109:5487–5492 Available at: http://www.ncbi.nlm.nih.gov/pubmed/22431587 [Accessed October 26, 2017].

Gordon PC, Meyer DE (1987) Control of serial order in rapidly spoken syllable sequences. J Mem Lang 26:300–321 Available at: http://www.sciencedirect.com/science/article/pii/0749596X87901161 [Accessed September 13, 2015].

Greenwald AG (1972) On doing two things at once: Time sharing as a function of ideomotor compatibility. J Exp Psychol 94:52–57 Available at: http://psycnet.apa.orgjournals/xge/94/1/52 [Accessed September 13, 2015].

Greicius MD, Krasnow B, Reiss AL, 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 Available at: http://www.ncbi.nlm.nih.gov/pubmed/12506194 [Accessed October 26, 2017].

Hairston WD, Hodges DA, Casanova R, Hayasaka S, Kraft R, Maldjian JA, Burdette JH (2008) Closing the mind□s eye: deactivation of visual cortex related to auditory task difficulty. Neuroreport 19:151–154 Available at: http://content.wkhealth.com/linkback/openurl?sid=WKPTLP:landingpage&an=00001756-200801220-00004 [Accessed July 25, 2017].

Henry FM, Rogers DE (1960) Increased Response Latency for Complicated Movements and A “Memory Drum” Theory of Neuromotor Reaction. Res Quarterly Am Assoc Heal Phys Educ Recreat 31:448–458 Available at: http://www.tandfonline.com/doi/abs/10.1080/10671188.1960.10762052#.VfV7YHghun0 [Accessed September 13, 2015].

Ingvar DH (1979) "Hyperfrontal" distribution of the cerebral grey matter flow in resting wakefulness; on the functional anatomy of the conscious state. Acta Neurol Scand 60:12–25 Available at: http://www.ncbi.nlm.nih.gov/pubmed/495039 [Accessed October 26, 2017].

James W (1890) The Principles of Psychology, Volume 1. H. Holt. Available at: https://books.google.co.uk/books/about/The_Principles_of_Psychology.html?id=JLcAAAAAMAAJ&pgis=1 [Accessed September 13, 2015].

Jeannerod M (1988) The neural and behavioural organization of goal-directed movements. Oxford psychology series, No. 15. Clarendon Press.

Keele, S. W., Cohen, A., & Ivry R (1990) Motor programs: Concepts and issues. In M. Jeannerod (Ed.),Attention and Performance Xiii: Motor Representation and Control. Taylor & Francis. Available at: https://books.google.com/books?id=c_0kAQAAMAAJ&pgis=1 [Accessed September 13, 2015].

Koch I, Hoffmann J (2000) Patterns, chunks, and hierarchies in serial reaction-time tasks. Psychol Res 63:22–35 Available at: http://www.ncbi.nlm.nih.gov/pubmed/10743384 [Accessed November 18, 2016].

Kruglanski AW, Kopetz C (2009) What is so special (and nonspecial) about goals?: A view from the cognitive perspective. In: The Psychology of Goals (Gordon B. Moskowitz HG, ed), pp 27–55.

Lewin K (1926) Vorsatz, Wille und Bedürfnis. Psychol Forsch 7:330–385 Available at: http://link.springer.com/10.1007/BF02424365 [Accessed September 13, 2015].

Lien M-C, Ruthruff E (2004) Task Switching in a Hierarchical Task Structure: Evidence for the Fragility of the Task Repetition Benefit. J Exp Psychol Learn Mem Cogn 30:697–713 Available at: http://www.ncbi.nlm.nih.gov/pubmed/15099137 [Accessed December 4, 2017].

Linke AC, Vicente-Grabovetsky A, Cusack R (2011) Stimulus-specific suppression preserves information in auditory short-term memory. Proc Natl Acad Sci U S A 108:12961–12966 Available at: http://www.ncbi.nlm.nih.gov/pubmed/21768383 [Accessed October 26, 2017].

Logan GD, Gordon RD (2001) Executive control of visual attention in dual-task situations. Psychol Rev 108:393–434 Available at: http://www.ncbi.nlm.nih.gov/pubmed/11381835 [Accessed February 17, 2017].

Manly T, Robertson IH, Galloway M, Hawkins K (1999) The absent mind: further investigations of sustained attention to response. Neuropsychologia 37:661–670 Available at: http://www.ncbi.nlm.nih.gov/pubmed/10390027 [Accessed October 26, 2017].

Mason MF, Norton MI, Van Horn JD, Wegner DM, Grafton ST, Macrae CN (2007) Wandering minds: the default network and stimulus-independent thought. Science 315:393–395 Available at: http://www.ncbi.nlm.nih.gov/pubmed/17234951 [Accessed October 26, 2017].

Mayr U, Kliegl R (2000) Task-set switching and long-term memory retrieval. J Exp Psychol Learn Mem Cogn 26:1124–1140 Available at: http://doi.apa.org/getdoi.cfm?doi=10.1037/0278-7393.26.5.1124 [Accessed March 8, 2017].

Merabet LB, Swisher JD, McMains SA, Halko MA, Amedi A, Pascual-Leone A, Somers DC (2006) Combined Activation and Deactivation of Visual Cortex During Tactile Sensory Processing. J Neurophysiol 97:1633–1641 Available at: http://www.ncbi.nlm.nih.gov/pubmed/17135476 [Accessed January 26, 2017].

Meyer DE, Kieras DE (1997) A computational theory of executive cognitive processes and multiple-task performance: Part 1. Basic mechanisms. Psychol Rev 104:3–65 Available at: http://www.ncbi.nlm.nih.gov/pubmed/9009880 [Accessed December 4, 2017].

Miller GA, Galanter E, Pribram KH (n.d.) Plans and the structure of behavior.

Monsell S (2003) Task switching. Trends Cogn Sci (Regul Ed) 7:134–140 Available at: http://www.ncbi.nlm.nih.gov/pubmed/12639695 [Accessed December 19, 2011].

Nirkko AC, Ozdoba C, Redmond SM, Bürki M, Schroth G, Hess CW, Wiesendanger M (2001) Different Ipsilateral Representations for Distal and Proximal Movements in the Sensorimotor Cortex: Activation and Deactivation Patterns. Neuroimage 13:825–835.

Povel D-J, Collard R (1982) Structural factors in patterned finger tapping. Acta Psychol (Amst) 52:107–123 Available at: http://www.sciencedirect.com/science/article/pii/0001691882900294 [Accessed September 13, 2015].

Prinz W (1987) Ideo-motor action. In: Perspectives on perception and action, ed. H. Heuer & A. F. Sanders. In: Perspectives on perception and action (Heuer H, Sanders F, eds), pp 47–76. Hillsdale, NJ: Lawrence Erlbaum Associates.

Raichle ME, MacLeod AM, Snyder AZ, Powers WJ, Gusnard DA, Shulman GL (2001) A default mode of brain function. Proc Natl Acad Sci U S A 98:676–682 Available at: http://www.ncbi.nlm.nih.gov/pubmed/11209064 [Accessed February 4, 2017].

Rogers RD, Monsell S (1995) Costs of a predictible switch between simple cognitive tasks. J Exp Psychol Gen 124:207–231 Available at: http://doi.apa.org/getdoi.cfm?doi=10.1037/0096-3445.124.2.207 [Accessed December 4, 2017].

Rosenbaum DA, Kenny SB, Derr MA (n.d.) Hierarchical control of rapid movement sequences. Available at: http://psycnet.apa.orgjournals/xhp/9/1/86 [Accessed October 27, 2014].

Schank RC, Abelson RP (1977) Scripts, plans, goals, and understanding□: an inquiry into human knowledge structures. L. Erlbaum Associates.

Schmidt RA, A. R (1975) A schema theory of discrete motor skill learning. Psychol Rev 82:225–260 Available at: http://content.apa.org/journals/rev/82/4/225 [Accessed February 3, 2017].

Schneider DW, Logan GD (2006) Hierarchical control of cognitive processes: Switching tasks in sequences. J Exp Psychol Gen 135:623–640 Available at: http://www.ncbi.nlm.nih.gov/pubmed/17087577 [Accessed December 4, 2017].

Schneider DW, Logan GD (2015) Chunking away task-switch costs: a test of the chunk-point hypothesis. Psychon Bull Rev 22:884–889 Available at: http://www.ncbi.nlm.nih.gov/pubmed/25214458 [Accessed September 13, 2015].

Shallice T, Cooper R (2011) The Organisation of Mind. Oxford University Press. Available at: http://books.google.com/books?hl=en&lr=&id=hb5rovNry_EC&pgis=1 [Accessed October 7, 2014].

Shulman GL, Fiez JA, Corbetta M, Buckner RL, Miezin FM, Raichle ME, Petersen SE (1997) Common Blood Flow Changes across Visual Tasks: II. Decreases in Cerebral Cortex. J Cogn Neurosci 9:648–663 Available at: http://www.ncbi.nlm.nih.gov/pubmed/23965122 [Accessed October 26, 2017].

Simony E et al. (2016) Dynamic reconfiguration of the default mode network during narrative comprehension. Nat Commun 7:12141 Available at: http://www.nature.com/doifinder/10.1038/ncomms12141 [Accessed January 10, 2017].

Spreng RN, Mar RA, Kim ASN (2009) The Common Neural Basis of Autobiographical Memory, Prospection, Navigation, Theory of Mind, and the Default Mode: A Quantitative Meta-analysis. J Cogn Neurosci 21:489–510 Available at: http://www.ncbi.nlm.nih.gov/pubmed/18510452 [Accessed October 26, 2017].

Sternberg, S., Monsell, S., Knoll, R. L., & Wright CE (1978) The latency and duration of rapid movement sequences: Comparisons of speech and typewriting. In G. E. Stelmach (Ed.), Information processing in motor control and learning (pp. 117–152). Elsevier Science. Available at: https://books.google.com/books?id=5qs5AwAAQBAJ&pgis=1 [Accessed

September 13, 2015].