Large-scale network interactions involved in dividing attention between the external environment and internal thoughts to pursue two distinct goals

David Maillet[1,*], **Roger E. Beaty**[2], **Aaron Kucyi**[3], and **Daniel L. Schacter**[4]

[1.]Rotman Research Institute, Baycrest Health Sciences, University of Toronto, 3560 Bathurst St, North York, ON M6A 2E1,

[2.]Department of Psychology, Pennsylvania State University, 140 Moore Building, University Park, PA 16801,

[3.]Neurology and Neurological Sciences, Stanford University, 300 Pasteur Drive, room M030 Stanford, CA 94305-2200 USA,

[4.]Department of Psychology, Harvard University, William James Hall, 33 Kirkland Street, Cambridge, MA 02138,

Abstract

Previous research suggests that default-mode network (DMN) and dorsal attention network (DAN) are involved in internally- and externally-directed attention, respectively, through interactions with salience network (SN) and frontoparietal network (FPCN). Performing a task requiring external attention is often accompanied by a down-regulation of attention to internal thoughts, and vice-versa. In contrast, we often divide our attention between the external environment and internal thoughts to pursue distinct goals, yet virtually no prior research has examined how brain networks support this functionally critical neurocognitive process. In the current study, participants planned their responses for an upcoming alternate uses divergent thinking task (AUT-Condition), indicated whether arrows were pointing left or right (Arrows-Condition) or performed both tasks simultaneously (Dual-Task condition). Behaviorally, the Dual-Task condition was associated with equivalent generation of alternate uses but increased RT variability compared to the single-task conditions. Static connectivity analyses indicated that FPCN and SN increased their connectivity to DMN and reduced their connectivity to DAN during the Dual-Task condition and the AUT-Condition compared to the Arrows-Condition. Furthermore, DAN-SN connectivity was highest during the Arrows-Condition, intermediate during the Dual-Task condition and lowest during the AUT-Condition. Finally, time-varying connectivity analyses indicated that individuals who reported spending less time thinking of alternate uses during the Dual-Task condition spent more time in a state associated with performing the Arrows-Condition. Overall, our results suggest that interactions between DMN, FPCN, SN and DAN allow internal-external dual-tasking, and that

[*]Corresponding Author: davidmaillet@gmail.com, 416-785-2500 ×3439.

time-varying functional connectivity between these networks is sensitive to attentional fluctuations between tasks during dual-tasking.

Keywords

Dual-tasking; creativity; divergent thinking; time-varying connectivity; salience network

1. Introduction

In many situations, performing externally-directed attention tasks requires down-regulation of attention to internal thoughts, and vice-versa. For instance, mind-wandering often interferes with performance on tasks requiring externally-directed attention (Smallwood & Schooler, 2006, 2015). By contrast, processing distracting environmental stimuli reduces the efficacy of long-term memory retrieval (Wais & Gazzaley, 2014). At the neural level, it is now established that two large-scale brain networks, the dorsal attention network (DAN; including regions such as frontal eye fields and superior parietal lobes) and the default-mode network (DMN; including regions such as medial prefrontal cortex, posterior cingulate and inferior parietal lobes) are associated with external and internal attention, respectively (Buckner, Andrews-Hanna, & Schacter, 2008; Fox et al., 2005; Fransson, 2006; Raichle, 2015; Shulman et al., 1997). These networks often display opposite patterns of activation in response to task demands. That is, performance of a variety of tasks requiring externally-directed attention is accompanied by increased DAN activation and DMN deactivation (Hampson, Driesen, Roth, Gore, & Constable, 2010; Shulman et al., 1997; Toro, Fox, & Paus, 2008) whereas performance of internally-directed attention tasks is associated with increased DMN activation (Buckner et al., 2008; Spreng, Mar, & Kim, 2009) and reduced DAN activation (Benedek et al., 2016).

Two other brain networks, the frontoparietal control network (FPCN) and the salience network (SN), interact with DMN and DAN to support the goal-directed allocation of attention internally or externally (Beaty, Benedek, Kaufman, & Silvia, 2015; Cole et al., 2013; Seeley et al., 2007; Spreng, Stevens, Chamberlain, Gilmore, & Schacter, 2010; Vincent, Kahn, Snyder, Raichle, & Buckner, 2008). SN and FPCN have been implicated in domain-general processes involved in sustaining attention and cognitive control that can support either internally-directed or externally-directed cognition. For instance, in one study (Spreng et al., 2010) participants performed an autobiographical planning task (requiring internal attention), a tower of London planning task (requiring external attention) and a low-level control task. DMN was activated to a greater extent during autobiographical planning versus the tower of London task, suggesting a role in internal attention, whereas DAN displayed the opposite pattern of activation, suggesting a role in external attention. In contrast, FPCN and SN were similarly activated during both the autobiographical planning and tower of London tasks compared to the low-level control task. Moreover, FPCN and SN increased their coupling to DMN and decreased their coupling to DAN during the internal planning task, but exhibited the reverse coupling pattern during the external planning task, thereby suggesting that these networks preferentially couple with either DAN or DMN depending on task demands. Although SN and FPCN behave similarly across many

conditions, a few studies have found that their connectivity can be dissociated. For instance, one study found that FPCN was sensitive to the occurrence of specific trials within a task, suggesting a role in trial-by-trial adaptive cognitive control, whereas SN was activated across trial types, suggesting a role in task-set maintenance (Dosenbach et al., 2007; Dosenbach et al., 2006).

Although much has been learned about how DMN, DAN, SN and FPCN support the deployment of attention internally or externally, these networks have often been studied in situations that require internally-directed or externally-directed attention exclusively. As reviewed above, such situations are often accompanied by a down-regulation of attention to the unattended modality. In contrast, even though we often divide our attention between the external environment and internal thoughts to pursue distinct goals, virtually no prior research has examined how brain networks support this functionally critical neurocognitive process. For instance, imagine a situation in which an individual is driving to work while simultaneously trying to generate solutions to a problem they are going to encounter later in the day. In such a situation, the individual has two simultaneous goals: driving, a task requiring externally-directed attention, and generating solutions, a task requiring internally-directed attention. It remains unknown how interactions between DMN, DAN, SN and FPCN reconfigure during this type of internal-external dual-tasking that is common in various contexts. The first goal of the current study was to provide insight into the nature of such network reconfigurations.

Although network interactions subserving internal-external dual-tasking have not been studied extensively, many studies have examined the neural correlates of dual-tasking involving two perceptually-based tasks (Alavash, Hilgetag, Thiel, & Giessing, 2015; Alavash, Thiel, & Giessing, 2016; Jiang, 2004; Nijboer, Borst, van Rijn, & Taatgen, 2014; Szameitat, Vanloo, & Muller, 2016). Dual-tasking often comes at a behavioral cost compared to performing tasks in isolation, and a general principle that has emerged from this literature is that such behavioral costs emerge to the extent that the neural correlates of the two single tasks overlap. That is, single-task activation similarity correlates with dual-tasking costs (Nijboer et al., 2014). With regard to internal-external dual-tasking, we hypothesized that potential interference between the two tasks would occur at the level of interactions between SN/FPCN and DMN/DAN. That is, whereas FPCN and SN may preferentially couple with DMN during the internal condition, the networks may instead preferentially couple with DAN during the external condition. Dual-tasking may result in interference to the extent that SN and FPCN cannot preferentially couple to DMN and DAN due to the requirement to split attention.

The second goal of this study was to assess how attention might fluctuate between the internal and external tasks over the course of the dual-task condition. In the real-life example of actively generating solutions to a problem while driving discussed earlier, some level of external attention is required throughout (to avoid crashing one's car), whereas generating solutions may occur more haphazardly. Thus, the driver may alternate between periods where she is dual-tasking and periods where she is only focused on the external driving task. Similarly, in the current study, the external task required constant attention whereas the internal task had no such requirement. Specifically, the external task required participants to

judge whether arrows presented every 1.5 seconds were pointing left or right (Arrows-Condition). The internal task was the alternate uses task, a widely-used and well-validated assessment of divergent creative thinking (AUT-Condition; Guilford, 1967). In this task, participants must come up with as many alternate uses as they can for common objects such as "fork". We chose this task because participants can keep generating alternate uses over long periods of time. In the Dual-Task condition, we expected that participants would fluctuate between time periods during which they are effectively dual-tasking (performing the arrows task and thinking of alternate uses) and time periods in which they are performing the arrows task without thinking of alternate uses.

To assess attentional fluctuations behaviorally, we asked participants to subjectively estimate the amount of time they spent thinking of alternate uses during dual-tasking. Neurally, we assessed time-varying connectivity (Calhoun, Miller, Pearlson, & Adali, 2014; Hutchison et al., 2013) using k-means clustering on sliding connectivity windows (Allen et al., 2014). Rather than averaging over the entire duration of a task or resting-state scan, time-varying connectivity assesses connectivity over shorter time-scales, and how connectivity changes over time. Increasing evidence suggests that time-varying connectivity is sensitive to spontaneous cognitive processes (Kucyi, Tambini, Sadaghiani, Keilholz, & Cohen, 2018). For instance, during a finger-tapping task, Kucyi, Hove, Esterman, Hutchison, and Valera (2017) found that tapping fluctuated between periods of high and low variability, and that periods of higher variability (which may signal attentional lapses) were associated with increasing time-varying connectivity between DMN and SN regions. In the current study, during the Dual-Task condition, the presence of connectivity patterns similar to those in the AUT-condition may indicate that participants are thinking of alternate uses, whereas the presence of connectivity patterns similar to the Arrows-Condition may indicate that participants are not thinking of alternate uses. We tested the hypothesis that time spent in such connectivity states during the Dual-Task condition would be related to the subjective estimates of time spent thinking of alternate uses, and that they may also be related to objective measures of task performance, which would suggest that time-varying connectivity can detect spontaneous moment-to-moment changes in attention over the course of the dual-tasking condition.

2. Methods

2.1. Participants

The experimental protocol was approved by the Institutional Review Board of Harvard University. Informed consent was obtained prior to participation. To determine the sample size for the current study, we conducted a pilot study in 32 participants to estimate the effect sizes of our desired behavioral effects. Specifically, we designed the Dual-Task condition such that: 1) generation of alternate uses, measured through fluency, would improve compared to baseline (providing objective evidence that participants are thinking of alternate uses during the Dual-Task condition) and 2) a behavioral cost, measured through mean RT and RTcov (RT standard deviation / mean RT), would be observed on the arrows task in the Dual-Task condition versus the Arrows-Condition. Note that, instead of the arrows task, we initially tried an odd/even task, but many pilot participants reported that dual-tasking was too

challenging, and that they therefore did not try to think of alternate uses while doing the odd/ even task. For this reason, we opted for the simpler arrows task.

Power analyses conducted on data from the 32 pilot participants with a = 0.05 and b = 0.80 suggested that 27 participants were required for the fluency effect, 16 participants were required for the mean RT effect, and 20 participants were required for the RTcov effect. Based on these numbers we aimed to recruit a minimum of 27 usable participants, and continued recruiting until D. Maillet left the lab of D. Schacter following the completion of his postdoc.

A total of thirty-five young adults were recruited for the current study. Four participants were excluded, one due to a computer crash, one for being a behavioral outlier on accuracy in the arrows task in the Arrows-Condition (Z = –4.42), one for being a behavioral outlier on accuracy in the arrows task in the Dual-Task condition (Z = –5.27), and one for excessive head movement (Z = 3.6 for mean relative displacement). Thus 31 adults (22 female, mean age = 23 (SD = 3.55), mean education = 15.50, (SD = 1.95)) were included in all analyses. All were right-handed, and none reported any history of psychological or neurological problems.

2.2. Tasks

The task design is illustrated in Figure 1. We use the terms Arrows-Condition and AUT-Condition to refer to the single-task conditions, and "arrows task" and "AUT" to refer to the tasks themselves, which participants also performed together during the Dual-Task condition. In the Arrows-Condition, participants were presented with 213 trials, each consisting of 5 arrows (all pointing left or pointing right) for 750ms, with a 750ms inter-trial interval. They were asked to press one button if the arrows pointed left and another if they pointed right. fMRI data were collected during this time. Next, a screen appeared for 5 seconds telling the participant that the AUT was about to begin. The fMRI scanner was then turned off and participants were presented with a word and asked to come up with alternate uses for it. They verbally reported their responses for two minutes while the fMRI scanner was off. Participants' responses were recorded and subsequently transcribed. This condition is named Arrows-Condition because participants could not previously plan their responses to the AUT while doing the arrows task.

The Dual-Task condition was identical to the Arrows-Condition, except that participants were given the word for the upcoming AUT at the beginning of the arrows task. Specifically, in the Dual-Task condition, the word appeared during the first 5 trials of the arrows task whereas in the Arrows-condition, the string "XXXXX" appeared instead (see Figure 1). In the Dual-Task condition, knowing the word for the upcoming AUT allowed participants to plan their responses while simultaneously doing the arrows task. Importantly, participants silently thought of their AUT responses while performing the arrows task and only verbally reported them following completion of the arrows task. The AUT-Condition was identical to the Dual-Task condition, except that participants were told not to respond to the arrows, so they could focus exclusively on planning their responses to the AUT. Participants were asked to keep their eyes open and looking at the screen during this task. Following the completion of all task runs, participants were asked to rate the extent to which they had exhibited

thoughts unrelated to the tasks on 1–5 scale (1 = *almost none*, 5 = *almost all*). Following the end of the AUT-Condition and the Dual-Task conditions, they were also asked to rate the extent to which they had thought about the AUT on the same 1–5 scale.

In total, participants completed 6 AUT sessions (2 in the Arrows-Condition, 2 in the AUT-Condition and 2 in the Dual-Task condition). The 6 words used for the AUT were common objects used in prior fMRI studies (e.g., Beaty et al., 2015): fork, ruler, broom, earring, ashtray and shoe. Assignment of the words to each condition was counterbalanced across subjects.

2.3. Procedure

Participants completed two runs of each of the three conditions. Two resting-state runs, presented at the beginning and end of the scanning session, were collected but are not discussed here. Prior to the fMRI session, participants received instructions for the upcoming tasks and practiced 100 trials of the arrows task, and practiced the AUT using the word "baseball" outside the scanner.

2.4. MRI data acquisition

Functional and anatomical images were acquired at the Harvard Center for Brain Science using a 3 Tesla Siemens Prisma scanner equipped with a 32-channel head coil. Anatomical images were acquired with a magnetization-prepared rapid gradient echo sequence (matrix size of 256×256, voxel size of 1 mm^3, 176 slices, TR = 2530ms, TE = 1.64ms). Functional images were acquired with a multiband echo-planar imaging sequence (TR = 0.86 sec, TE = 25ms, 2.3mm^3 resolution, 60 slices, multiband factor of 4). This short TR sequence was chosen because of our interest in time-varying connectivity. 380 volumes were acquired in each of 8 runs (2 per condition).

2.5. Behavioral data analysis

The data used to perform all analyses in this manuscript are available at https://osf.io/ec5sh/. For behavioral and fMRI analysis, the first 12 trials of each condition were dropped (the 5 trials during which the AUT words or "XXXXX" strings were presented and the next 7 trials) so that task-related differences in behavior and connectivity could not be attributed to perceptual differences between task. This adjustment left 201 trials per run (just over 5 minutes). Thus, because there were 2 runs for each condition, 10 minutes of behavioral and fMRI data per condition were analyzed. For the arrows task, prior to behavioral analysis, trials with RTs that were 3 standard deviations away from the mean of each run were discarded. We analyzed task-related differences in accuracy, mean RT and RTcov between the Arrows-Condition and the Dual-Task conditions. RTcov is calculated by dividing RT standard deviation by mean RT (Stuss, Murphy, Binns, & Alexander, 2003). For RT analyses, only correct trials were used to calculate these metrics.

For the AUT, we calculated three measures commonly used in the creativity literature: fluency, categories of appropriate uses and originality. Fluency refers to the number of ideas generated by participants. Categories of appropriate use is a measure that differs from fluency in two ways. First, it discards inappropriate uses (e.g. a shoe can be used to hold an

adult). Second, it groups together conceptually similar ideas (e.g. a fork can be used to defend yourself from an intruder, a fork can be used as a weapon against an animal) and therefore provides a count of different categories of ideas. The third measure was originally rating, which provides an index of a response's creative quality (i.e., novelty, uncommonness, remoteness), using a 1–5 scale (1 = not at all creative, 5 = very creative; Silvia et al., 2008). Two raters blind to the task conditions rated each response for categories of appropriate uses and originality. We calculated intra-class correlations to assess reliability of these ratings between the two raters. For analyses of task-related differences in categories of appropriate uses and originality, we averaged the two raters' scores.

2.6. fMRI preprocessing

fMRI data were preprocessed in FSL 5.0.4. The first 4 scans of each run were deleted. Brain extraction (BET), realignment of each volume to the middle volume (MCFLIRT), and spatial smoothing (6-mm full width at half-maximum kernel) were performed. We then submitted the data to ICA-AROMA, an automated tool for motion-artifact removal, shown to improve sensitivity and specificity of fMRI activation and connectivity analyses (Pruim, Mennes, Buitelaar, & Beckmann, 2015; Pruim, Mennes, van Rooij, et al., 2015). Briefly, this analysis involved running independent components analysis (ICA, with automatic dimensionality estimation using MELODIC), identification of motion-relevant components (based on correlation with realignment parameters, spatial content in CSF and edge voxels, and high-frequency temporal content), and regression of the motion-relevant components from the data. Finally, a high-pass (0.01 Hz cutoff) temporal filter was applied. Functional MRI data were registered to T1 and standard MNI152 space using linear transformations (FLIRT) with 6 and 12 df, respectively.

2.7. fMRI analysis

2.7.1. Static functional connectivity—We used the 100-area, 7-network parcellation from Schaefer et al. (2018) in MNI152 space to define regions of interest (ROI). The mean BOLD time series from voxels within each of sixty-four regions labeled in this parcellation as belonging to the DMN, DAN, FPCN and SN were extracted and used to compute a Fisher-transformed correlation matrix, separately for each run. The matrices the two runs for each of the four conditions were averaged. Next, we averaged together all correlations between any two networks (e.g. we averaged all the correlations between individual DMN-DAN ROIs, resulting in a single DMN-DAN value per subject, per task). Thus, in total, there were six between-network values per subject per task: DMN-DAN, DMN-FPCN, DMN-SN, DAN-FPCN, DAN-SN and FPCN-SN. We submitted data from each between-network connectivity analysis to a one-way repeated measures ANOVA. We considered a result significant if it reached a $p < 0.008$ threshold (Bonferroni corrected for 6 multiple comparisons).

We also conducted exploratory analyses using the 100-area, 17-network parcellation from Schaefer et al. (2018). Although our primary interest was in interactions between large-scale networks, potentially important information may come from examining sub-network interactions. In the 17-network parcellation, DMN in subdivided into three sub-networks, DAN is sub-divided into two sub-networks, FPCN is subdivided into three sub-networks and

SN is subdivided into two networks, yielding a total of 45 between-network comparisons. These analyses are reported in the Supplementary Materials.

2.7.2. Time-varying functional connectivity—Runs were split into connectivity windows, with the onset of each window progressively shifted by 0.86sec (1TR) from the previous window. Previous studies have used connectivity windows of different lengths, and there is uncertainty as to which length may be optimal for detecting cognitive processes (Hutchison et al., 2013). In the current study, we conducted analyses with 30s, 60s and 90s windows, similar to durations used in other work (Allen et al., 2014; Kucyi & Davis, 2014; Mooneyham et al., 2017; Wang, Ong, Patanaik, Zhou, & Chee, 2016). Window size had little effect on most of the results. Therefore, in the Results section, we present analyses for 60sec windows (an intermediate value). Additional information regarding results using 30sec and 90sec windows can be found in Supplemental Materials.

Connectivity matrices were created in the same way described for static connectivity, but with multiple windows per run, rather than averaged across the entire run. For each temporal window in each scan, an ROI-by-ROI connectivity matrix (Fisher-transformed) was constructed, with bottom triangle and diagonal elements deleted. Retained values were then transformed to a vector for each temporal window, and vectors were concatenated across conditions, runs and subjects. Thus, the input matrix for kmeans clustering consisted of ROI pairs as rows and temporal windows as columns. This matrix was submitted to k-means clustering with 100 iterations to identify a small pre-specified number of connectivity states. Every time window for each individual participant was assigned to one of the states identified at the group level.

Few guidelines exist as to how many k connectivity states should be specified for such an analysis. Our strategy was to use the minimal number of states necessary to yield task-related differences in time spent in the different states (i.e. the minimal number of states that were sensitive to our behavioral tasks). Using k=2, no task differences in time spent in the two states were observed, perhaps because two states is too few to properly characterize this dataset. Using k=3 states, we did find task-related differences in time spent in the three states, which we report in the Results section. Because this choice of k is somewhat arbitrary, we also performed analyses using k=4 and k=5 to assess the stability of the results. Generally, the main results using k=3 were stable when using k=4 and k=5 states (these analyses are presented in the Supplementary Materials). The time-varying metric of interest was the number of time windows (time) spent in each state. Task-related differences in time spent in each state was assessed using a one-way repeated measures ANOVA. Correlations between time spent in each state and behavioral measures of interest were also performed.

3. Results

3.1. Behavioral Results

3.1.1. Arrows task—Only the Arrows-Condition and the Dual-Task condition included the arrows task, whereas the AUT-condition did not. Behavioral data for the arrows task are presented in Table 1 and Figure 3. Participants' accuracy was high and did not differ between the two conditions, $t(1,30) = 0.91$, $p = 0.37$, $d = 0.16$. Unlike our independently

conducted pilot study, there was no significant task-related difference in mean RT, $t(1,30) = 1.75$, $p = 0.09$, $d = 0.31$, although there was a trend in the expected direction. However, replicating our pilot results, RTcov was significantly higher in the Dual-Task versus the Arrows-Condition, $t(1,30) = 2.49$, $p = 0.02$, $d = 0.45$). Thus, in summary, for the arrows task, the Dual-Task condition was associated with only minor behavioral costs compared to the Arrows-Condition: there was a small increase in RTcov but no change in mean RT or accuracy.

3.1.2. AUT task—For the AUT, we calculated task-related differences in fluency, categories of appropriate uses and originality using three one-way repeated measures ANOVAs. Behavioral data for the AUT is presented in Table 1 and Figure 2. Participants performed the AUT in three conditions: AUT-condition, Dual-Task and Arrows-Condition. Participants could plan their responses ahead of time in the AUT-condition and Dual-Task conditions, but not in the Arrows-Condition, which served as a baseline for AUT performance. For fluency, there was a significant effect of task, $F(2,60) = 26.30$, $p < 0.001$, $\eta^2 p = 0.47$. Post-hoc tests indicated that compared with the Arrows-Condition, fluency was higher in the Dual-Task condition, $t(1,30) = 5.81$, $p < 0.001$, $d = 1.04$, and the AUT-condition, $t(1,30) = 6.38$, $p < 0.001$, $d = 1.15$. There was no difference in fluency between the Dual-Task condition and the AUT-condition, $t(1,30) = 0.05$, $p = 0.96$, $d = 0.01$.

Categories of appropriate uses were scored by two raters. We calculated the intra-class correlation (ICC) for each of the three tasks separately. The average ICC across tasks was 0.93, indicating excellent agreement between raters. The values for categories of appropriate uses were averaged across the two raters and this average was used for subsequent analysis. A one-way repeated measures ANOVA revealed a main effect of task, $F(2,60) = 15.90$, $p < 0.001$, $\eta^2 p = 0.35$. Post-hoc tests indicated that compared with the Arrows-Condition, individuals generated more categories of appropriate use in the Dual-Task condition, $t(1,30) = 4.65$, $p < 0.001$, $d = 0.84$, and the AUT-Condition, $t(1,30) = 4.74$, $p < 0.001$, $d = 0.85$. There was no difference in categories of appropriate use between the Dual-Task condition and the AUT-Condition, $t(1,30) = 1.14$, $p = 0.27$, $d = 0.20$.

For originality, the average ICC across tasks was 0.57, indicating fair agreement between raters. The values for categories of appropriate uses were averaged across raters and this average was used for subsequent analysis. The one-way repeated measures ANOVA was not significant, $F(2,60) = 1.23$, $p = 0.30$, $\eta^2 p = 0.04$.

In summary, participants improved on the objective measures of the AUT (fluency and categories of appropriate uses) in the two conditions in which they could plan their responses (Dual-Task and AUT-Condition) compared to their baseline performance, providing objective evidence that they engaged in planning.

3.1.3. Subjective ratings—Following completion of the Dual-Task condition and the AUT-Condition, participants were asked to indicate the extent to which they had thought about the AUT (Figure 2g). There was a trend for more thoughts about the AUT in the AUT-Condition versus the Dual-Task condition, $t(1,30) = 1.99$, $p = 0.06$, $d = 0.36$.

Following completion of all tasks, participants were asked the extent to which they had exhibited task-unrelated thoughts (Figure 2h). The one-way repeated measures ANOVA was significant, $F(2,60) = 10.2$, $p < 0.001$, $n^2p = 0.25$. Post-hoc tests indicated that participants reported exhibiting more task-unrelated thoughts in the Arrows-Condition compared to the Dual-Task condition, $t(1,30) = 3.85$, $p < 0.001$, $d = 0.69$) and the AUT-Condition, $t(1,30) = 3.05$, $p = 0.005$, $d = 0.55$). There were no differences in task-unrelated thoughts between the Dual-Task and the AUT-Condition, $t(1,30) = 1.27$, $p = 0.21$, $d = 0.23$.

3.2. fMRI results

Static connectivity data are presented in Figure 3 and Table 2. The repeated measures ANOVA for DMN-SN connectivity was significant, $F(2,60) = 8.56$, $p < 0.001$, $n^2p = 0.22$. Post-hoc tests indicated that DMN-SN was lower during the Arrows-Condition compared to both the Dual-Task condition, $t(1,30) = 2.72$, $p = 0.01$, $d = 0.49$, and the AUT-Condition, $t(1,30) = 3.85$, $p < 0.001$, $d = 0.69$. There was no difference in DMN-SN connectivity between the Dual-Task condition and the AUT-Condition, $t(1,30) = 1.49$, $p = 0.15$, $d = 0.27$. The results for DMN-FPCN connectivity were very similar. That is, the ANOVA was significant, $F(2,60) = 8.52$, $p < 0.001$, $n^2p = 0.22$, and post-hoc tests indicated that this was due to DMN-FPCN connectivity being lower in the Arrows-Condition compared to both the Dual-Task condition, $t(1,30) = 3.34$, $p = 0.002$, $d = 0.60$, and the AUT-Condition, $t(1,30) = 3.72$, $p < 0.001$, $d = 0.67$. There was no differences in DMN-FPCN connectivity between the Dual-Task condition and the AUT-Condition, $t(1,30) = 0.79$, $p = 0.43$, $d = 0.14$.

The ANOVA for DAN-FPCN connectivity was significant, $F(2,60) = 18$, $p < 0.001$, $n^2p = 0.38$. Post-hoc tests indicated that DAN-FPCN connectivity was higher during the Arrows-Condition compared to the Dual-Task condition, $t(1,30) = 5.10$, $p < 0.001$, $n^2p = 0.92$ and the AUT-Condition, $t(1,30) = 4.87$, $p < 0.001$, $n^2p = 0.88$, whereas there was no difference between the Dual-Task condition and the AUT-Condition, $t(1,30) = 1.00$, $p = 0.32$, $n^2p = 0.18$.

The ANOVA for DAN-SN connectivity was significant, $F(2,60) = 15.2$, $p < 0.001$, $n^2p = 0.34$. Post-hoc tests indicated that DAN-SN connectivity was higher during the Arrows-Condition compared to both the Dual-Task condition, $t(1,30) = 3.06$, $p = 0.005$, $d = 0.55$, and the AUT-Condition, $t(1,30) = 5.07$, $p < 0.001$, $d = 0.91$. DAN-SN connectivity was also higher during the Dual-Task condition compared to the AUT-Condition, $t(1,30) = 2.75$, $p = 0.01$, $d = 0.49$. Lastly the ANOVA for DMN-DAN connectivity was not significant, $F(2,60) = 1.58$, $p = 0.21$, $n^2p = 0.05$, nor was the ANOVA for FPCN-SN, $F(2,60) = 0.22$, $p = 0.81$, $n^2p = 0.01$.

In summary, FPCN and SN increased their connectivity to DMN during the AUT-condition and the Dual-Task condition compared to the Arrows-Condition. On the other hand, FPCN increased its connectivity to DAN during the Arrows-Condition compared to the Dual-Task and the AUT-Condition. Finally, the only connection that was sensitive to both tasks was DAN-SN: DAN-SN was highest during the Arrows-Condition, at an intermediate level during the Dual-Task condition, and lowest during the AUT-Condition.

Previous studies in the dual-tasking literature have indicated that dual-tasking costs are attributable to overlapping patterns of neural recruitment between single-tasks. We thus assessed whether individual differences in DAN-SN connectivity were associated with task performance. The only behavioral cost associated with dual-tasking was an increase in RTcov in the arrows task. To test whether this increase in RTcov in the Dual-Task condition versus the Arrows-condition was associated with reduced DAN-SN connectivity, we correlated RTcov costs (RTcov in the Dual-Task condition minus the Arrows-Condition) with DAN-SN connectivity difference scores (Dual-Task connectivity minus Arrows-Condition connectivity). There was a negative correlation ($r = -0.36$, $p < 0.05$; Figure 4), indicating that reductions in DAN-SN connectivity in the Dual-Task condition versus the Arrows-Condition were indeed associated with greater RTcov costs. In other words, the individuals whose connectivity is most reduced during During-Task vs. Arrows-Condition have the highest RTcov cost.

3.2.5. Time-varying connectivity—During the Dual-Task condition, most participants reported that they did not think of the AUT for the entire block, suggesting that they alternated between time periods where they were performing the AUT and the arrows task concurrently and periods where they were doing the arrows task without thinking of the AUT. We performed time-varying connectivity analyses to assess whether we could identify connectivity states associated with these attentional fluctuations.

We used k-means clustering on 60 second connectivity windows from all conditions to identify three connectivity states (see Methods). The connectivity matrices associated with each state, as well as task-related differences in time spent in each state, are presented in Figure 6. We first assessed whether there were task-related differences in time spent in each state. For the first state, the ANOVA was significant, $F(2,60) = 55.3$, $p < 0.001$, $\eta^2 p = 0.65$. Post-hoc tests indicated that participants spent more time in this state in the Arrows-Condition compared to both the AUT-Condition, $t(1,30) = 8.21$, $p < 0.001$, $\eta^2 p = 1.48$ and the Dual-Task condition, $t(1,30) = 8.29$, $p < 0.001$, $\eta^2 p = 1.49$, with no difference between the AUT-Condition and the Dual-Task condition, $t(1,30) = 1.48$, $p = 0.15$, $\eta^2 p = 0.27$. We thus named this state the Arrows state. For the second state, the ANOVA was significant, $F(2,60) = 55.7$, $p < 0.001$, $\eta^2 p = 0.65$. Post-hoc tests indicated that participants spent less time in this state in the Arrows-Condition compared to both the AUT-Condition, $t(1,30) = 7.94$, $p < 0.001$, $\eta^2 p = 1.43$ and the Dual-Task condition, $t(1,30) = 8.75$, $p < 0.001$, $\eta^2 p = 1.57$ with no difference between the AUT-Condition and the Dual-Task condition, $t(1,30) = 0.58$, $p = 0.56$, $\eta^2 p = 0.11$. We thus named this state the AUT state. For State #3, the ANOVA was not significant, $F(2,60) = 0.36$, $p = 0.70$, $\eta^2 p = 0.01$. Although it is hard to explain what State #3 might refer to given that it was not sensitive to the experimental tasks, additional analyses indicated that time spent in this state in a given task was highly correlated to between-network static connectivity estimates for this task (most r values > 0.5). Time spent in the Arrows State and AUT State were less strongly related to static connectivity (most r values < 0.5). Thus, perhaps State # 3 represents time periods that were more noisy and harder to assign to one of the other two dynamic functional connectivity states.

The pattern of task-related differences reported in the previous paragraph held for different time window sizes and different number of states in the k-means clustering (see Supplementary Materials). We also conducted minute-by-minute analyses of time spent in each state to rule out the possibility that, in the Dual-Task condition, participants initially spent most of their time in the AUT state and then stopped thinking about the AUT and moved to the Arrows state. Inconsistent with this hypothesis, task-related differences in time spent in each state was constant across all minutes (Supplementary Materials).

Given concerns about the extent to which time-varying connectivity is attributable to head movement (Laumann et al., 2017), we assessed whether time spent in any state in any of the four conditions was correlated with head movement (3 states * 4 conditions = 12 correlations). None of the correlations passed a liberal $p < 0.05$ threshold. Thus, movement had a limited influence on time-varying connectivity.

Compared to the Arrows state, the AUT State was associated with more DMN-FPCN and DMN-SN connectivity but less DAN-FPCN and DAN-SN connectivity (Table 3 and Figure 5), which is reminiscent of the static connectivity differences associated performing the AUT conditions versus the Arrows-Task. Thus, one possibility is that time periods associated with the AUT State are periods where participants were thinking of the AUT whereas time periods associated with the Arrows state reflect time periods where participants are not thinking of the AUT. To more directly test this hypothesis, we assessed whether time spent in the AUT and Arrows states during the Dual-Task condition correlated with behavioral variables of interest. During the Dual-Task condition, time spent in the Arrows state was negatively correlated with subjective estimates of time thinking of the AUT (without controlling for movement: r = −0.42, p = 0.02; controlling for movement: r = −0.46, p = 0.01; Figure 6), whereas time spent in the AUT state was positively, but non-significantly related to this estimate (without controlling for movement: r = 0.26, p = 0.16; controlling for movement: r = 0.28, p = 0.14). The correlation between time spent in the Arrows state and subjective estimates of time spent thinking of the AUT also held when using 90 second time windows and when using a 4-state or a 5-state k-means solution (see supplementary material). Time spent in the Arrows state was also negatively correlated with AUT fluency improvement (r = −0.37, p = 0.04) whereas time spent in the AUT state was not associated with this value (r = 0.22, p = 0.23). However, the correlation between AUT fluency and time spent in the Arrows state did not hold when using k = 4 or 5 states in the k-means clustering, so appears less consistent. No significant correlations with time spent in State #3 were observed.

Lastly, in the Dual-Task condition, we also assessed whether there were differences in RTcov in time periods spent in the Arrows state versus the AUT state. We hypothesized that if these states reflect time periods where participants are, versus are not, thinking of the AUT, then RTcov may be higher during the AUT state versus the No-AUT state. Inconsistent with this hypothesis, in the Dual-Task condition, we found no differences in RTcov between time periods associated with the Arrows state (mean = 0.15, SD = 0.02) and the AUT state (mean = 0.15, SD = 0.02; t(1,28) = 0.32, p = 0.32). There also were no significant differences in RTcov between State # 3 and the other two states.

4. Discussion

Dividing attention between the external environment and internal thoughts to pursue distinct goals is a critically important neurocognitive process, yet little research has examined how brain networks support it. The current study was conducted to identify connectivity changes associated with internal-external dual-tasking compared to performing each task by itself. Behaviorally, participants performed the AUT equally well in the Dual-Task condition compared to the AUT-Condition. In contrast, the Dual-Task condition was associated with a cost in RTcov compared to the Arrows-condition. Whereas our pilot behavioral results indicated that participants also incurred a mean RT cost in the Dual-Task condition versus the Arrows-condition, in the fMRI study, this result was not significant when using 2-tailed statistics (p = 0.09). Because the current study was conducted to identify connectivity associated with competition between internal and external attention, and because the main way of inferring competition is through a behavioral cost of dual-tasking versus single-tasking, the fact that there were only small behavioral costs is a limitation of the current fMRI study. This should be kept in mind when interpreting the fMRI results, as it is possible that the use of different internal and external tasks yielding a greater amount of competition would have yielded different results from those observed here. In the following sections, we discuss the implications of the brain connectivity results associated with performing these tasks.

4.1. Connectivity changes associated with performing internally-directed and externally-directed attention tasks

Before discussing results pertaining to dual-tasking, we first start by discussing static connectivity results associated with performing the Arrows-Condition and the AUT-condition. Recent studies have assessed network interactions involved in performing internally-directed attention tasks. For instance, Spreng et al. (2010) reported that during an autobiographical planning task, FPCN and SN increased connectivity with the DMN but decreased their connectivity with DAN. In another study, Beaty et al. (2015) reported increased connectivity between a key region of DMN (posterior cingulate) and regions in both FPCN (dorsolateral prefrontal cortex) and SN (insula) during the AUT compared to a semantic control task. Consistent with this prior work, in the current study, performing the AUT (in the Dual-Task condition and AUT-condition versus Arrows-Condition) was associated with increased connectivity between DMN and both FPCN and SN. Moreover, sub-network analyses (reported in the Supplementary Materials) indicated that it was regions associated with the medial temporal lobe DMN subsystem (thought to be involved in memory-based processes, Andrews-Hanna, Reidler, Sepulcre, Poulin, & Buckner, 2010; Buckner et al., 2008, see also Konishi et al., 2015, Vatensever et al., 2017a; 2017b) and of the core DMN subsystem, but not of the dorsal medial prefrontal subsystem (thought to be involved in self-referential processes; Andrews-Hanna et al., 2010) that increased connectivity to FPCN and SN during the AUT. It has been suggested that interactions between DMN, FPCN and SN during creative cognition may reflect an interplay between generative and memory-based processes in the DMN, strategic functions of the FPCN, along with detection and attentional processes in SN (Beaty, Benedek, Silvia, & Schacter, 2016). Because participants needed not only to generate ideas but also to remember them to report

following the arrows task, increased connectivity between DMN and both FPCN and SN in the current study may also reflect maintenance/rehearsal of ideas. Performing the AUT was also associated with reduced connectivity between DAN and both FPCN and SN, which may reflect a decoupling of attention from the external environment during divergent-thinking. It is possible that down-regulation of external attention was necessary to inhibit the visual information on the screen (flashing arrows).

The only increase in connectivity associated with performing the Arrows-Condition compared to the AUT-condition was DAN-SN. In contrast, and unlike Spreng et al. (2010), FPCN did not exhibit increased connectivity with DAN when performing the externally-directed attention task. This difference between studies is likely attributable to differences in the external task used in each study. Spreng et al. used a Tower of London planning task, which requires considerable planning and cognitive control whereas in the current study, a much simple arrows task was used. FPCN may only increase its connectivity to DAN in tasks that require cognitive control to be used in the service of external attention. In contrast, SN may increase connectivity to DAN to sustain attention and/or support maintenance of a task-set associated with events in the external environment, regardless of the requirement for cognitive control (Dosenbach et al., 2007; Dosenbach et al., 2006). Also notable is that the Arrows-Condition was not accompanied by decreases in connectivity between DMN and FPCN and SN compared to the other two conditions. This outcome may be attributable to participants exhibiting a greater amount of task-unrelated thoughts in the Arrows-Condition compared to the AUT conditions.

4.2. Connectivity changes associated with internal-external dual-tasking

The first main goal of the current study was to assess how connectivity may reorganize to support internal-external dual-tasking compared to the performance of each task in isolation. We hypothesized that dual-tasking may result in behavioral costs to the extent to which FPCN and SN cannot preferentially couple with DMN and DAN due to the requirement to split attention. The only connection that was sensitive to both the internal and external tasks was DAN-SN. Connectivity in DAN-SN was highest during Arrows-Condition, intermediate during dual-tasking and lowest during AUT-Condition. Moreover, the reduction in DAN-SN connectivity in the Dual-Task versus the Arrows-Condition was correlated with increased RTcov costs. Given our small sample size and the small r value, this correlation should be interpreted with caution. However, it is consistent with the notion that overlap in neural recruitment between single-tasks are associated with dual-tasking costs (Nijboer et al., 2014). That the only overlap in connectivity patterns associated with the internal and external tasks involved SN is consistent with the suggestion that this network mediates between attention to endogenous and exogenous events (Bressler & Menon, 2010). One possibility is that SN is a bottleneck limiting our ability to simultaneously focus our attention to distinct internal and external events.

As alluded to earlier, in contrast with SN, FPCN connectivity was only modulated by the internal, but not the external task, likely because the latter task did not require much cognitive control. Notably, pilot testing indicated that if the external task was made harder (by using an odd/even judgment), most participants reported not engaging in dual-tasking

because it was too difficult. Thus, although speculative, it is likely that FPCN is another bottleneck that prevents internal-external dual-tasking from even taking place. That is, performing the AUT and an odd/even judgment simultaneously may have been too difficult due to both tasks depending on FPCN. This network may only be able to support the deployment of cognitive control to an externally-directed *or* an internally-directed attention task, but not both.

4.3. Time-varying connectivity during internal-external dual-tasking

The second main goal of our study was to assess how attention might fluctuate between the internal and external tasks over the course of the Dual-Task condition. In recent years, there has been increasing interest in using time-varying connectivity to assess spontaneous cognitive processes (Kucyi et al., 2018). For instance, it has been demonstrated that time-varying DMN connectivity is sensitive to mind-wandering and attentional lapses during ongoing task performance (Kucyi & Davis, 2014; Kucyi et al., 2017). In the current study, during the Dual-Task condition, most participants reported that they did not think of the AUT for the entire block, suggesting that they alternated between time periods where they were performing both the AUT and arrows task and time periods where they were doing the arrows task without the AUT. We performed time-varying connectivity analyses to assess whether we could identify connectivity states associated with these attentional fluctuations.

During the Dual-Task condition, participants spent the majority of the time in the AUT state, a state high in FPCN-DMN and SN-DMN connectivity, which was also common during the AUT-condition. However, in the Dual-Task condition, participants also sometimes visited the Arrows state, a state higher in FPCN-DAN and SN-DAN connectivity that was common during the Arrows-condition. Thus, during the Dual-Task condition, one possibility is that time spent in the AUT state reflected periods where participants were dual-tasking (performing both the arrows task and AUT) whereas time spent in the arrows state reflected periods where participants were only performing the arrows task without thinking of the AUT. Supporting this possibility, we found that time spent in the Arrows state was negatively correlated with participants' subjective estimates of time spent thinking of the AUT. The negative association between time spent in the Arrows state and subjective estimates of time spent thinking of the AUT was found across several window-sizes (60 second, 90 second) across 3- 4- and 5-state solutions, and with or without controlling for movement, supporting its robustness. Thus, participants that reported spending the most time dual-tasking were those that spent the least time in the connectivity state associated with performing the Arrows-Condition. In addition, this effect appeared specific to time-varying connectivity, as we were unable to find a correlation between this subjective estimate and any static connectivity measure. This result is consistent with other studies demonstrating behavioral associations with time-varying connectivity over-and-above static connectivity (e.g., Kucyi & Davis, 2014)

We also assessed in-the-moment associations between being in the Arrows state versus the AUT state and performance on the arrows task. Given the increase in RTcov between the entire Dual-Task condition compared to the Arrows-Condition, we hypothesized that we may be able to find a similar increase in RTcov *within* the Dual-Task condition, when

participants are in the AUT state versus the Arrows state. However, we did not find any significant difference between the two states. It is possible that the RTcov effect was too subtle to detect within the Dual-Task condition, or that such an effect would have been observed with a higher sample size.

5. Conclusion and Limitations

In conclusion, the results of the current study suggest that SN may be sensitive to the tradeoff between external and internal attention: SN-DAN was highest during the Arrows-Condition, at an intermediate level in the Dual-Task condition, and lowest during the AUT-Condition. Our results additionally provide some evidence that time-varying connectivity is sensitive to internal-external attentional fluctuations during-dual tasking: participants that report spending the most time thinking of the AUT spent less time in a connectivity state associated with performing the Arrows-Condition. A limitation of the current study is that we used only one combination of internal and external tasks, and it is possible that the results observed here would change using different tasks. In particular, with the tasks used here, the only behavioral cost observed was for RTcov, with no cost to mean RT or accuracy. It would be of interest to study internal-external dual-tasking using an external task that was more difficult than the one used here to assess whether FPCN would also become sensitive to the tradeoff between internal and external attention. Finally, whether attention can be biased to either the internal task or the external task using motivational incentives, and its impact on the patterns of connectivity observed here, is an interesting topic for future investigation.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgements

References

Alavash M, Hilgetag CC, Thiel CM, & Giessing C (2015). Persistency and flexibility of complex brain networks underlie dual-task interference. Hum Brain Mapp, 36(9), 3542–3562. [PubMed: 26095953]

Alavash M, Thiel CM, & Giessing C (2016). Dynamic coupling of complex brain networks and dual-task behavior. Neuroimage, 129, 233–246. [PubMed: 26803061]

Allen EA, Damaraju E, Plis SM, Erhardt EB, Eichele T, & Calhoun VD (2014). Tracking whole-brain connectivity dynamics in the resting state. Cereb Cortex, 24(3), 663–676. [PubMed: 23146964]

Andrews-Hanna JR, Reidler JS, Sepulcre J, Poulin R, & Buckner RL (2010). Functional-anatomic fractionation of the brain's default network. Neuron, 65(4), 550–562. [PubMed: 20188659]

Beaty RE, Benedek M, Kaufman SB, & Silvia PJ (2015). Default and Executive Network Coupling Supports Creative Idea Production. Sci Rep, 5, 10964. [PubMed: 26084037]

Beaty RE, Benedek M, Silvia PJ, & Schacter DL (2016). Creative Cognition and Brain Network Dynamics. Trends Cogn Sci, 20(2), 87–95. [PubMed: 26553223]

Benedek M, Jauk E, Beaty RE, Fink A, Koschutnig K, & Neubauer AC (2016). Brain mechanisms associated with internally directed attention and self-generated thought. Sci Rep, 6, 22959. [PubMed: 26960259]

Bressler SL, & Menon V (2010). Large-scale brain networks in cognition: emerging methods and principles. Trends Cogn Sci, 14(6), 277–290. [PubMed: 20493761]

Buckner RL, Andrews-Hanna JR, & Schacter DL (2008). The brain's default network: anatomy, function, and relevance to disease. Ann N Y Acad Sci, 1124, 1–38. [PubMed: 18400922]

Calhoun VD, Miller R, Pearlson G, & Adali T (2014). The chronnectome: time-varying connectivity networks as the next frontier in fMRI data discovery. Neuron, 84(2), 262–274. [PubMed: 25374354]

Cole MW, Reynolds JR, Power JD, Repovs G, Anticevic A, & Braver TS (2013). Multi-task connectivity reveals flexible hubs for adaptive task control. Nat Neurosci, 16(9), 1348–1355. [PubMed: 23892552]

Dosenbach NU, Fair DA, Miezin FM, Cohen AL, Wenger KK, Dosenbach RA, … Petersen SE (2007). Distinct brain networks for adaptive and stable task control in humans. Proc Natl Acad Sci U S A, 104(26), 11073–11078. [PubMed: 17576922]

Dosenbach NU, Visscher KM, Palmer ED, Miezin FM, Wenger KK, Kang HC, … Petersen SE (2006). A core system for the implementation of task sets. Neuron, 50(5), 799–812. [PubMed: 16731517]

Fox MD, Snyder AZ, Vincent JL, M. C, Van Essen DC, & Raichle ME (2005). The human brain is intrinsically organized into dynamic, anticorrelated functional networks. Proc Natl Acad Sci USA, 102, 9673–9678. [PubMed: 15976020]

Fransson P (2006). How default is the default mode of brain function? Further evidence from intrinsic BOLD signal fluctuations. Neuropsychologia, 44(14), 2836–2845. [PubMed: 16879844]

Guilford JP (1967). The nature of human intelligence. New York, NY: McGraw Hill.

Hampson M, Driesen N, Roth JK, Gore JC, & Constable RT (2010). Functional connectivity between task-positive and task-negative brain areas and its relation to working memory performance. Magn Reson Imaging, 28(8), 1051–1057. [PubMed: 20409665]

Hutchison RM, Womelsdorf T, Allen EA, Bandettini PA, Calhoun VD, Corbetta M, … Chang C (2013). Dynamic functional connectivity: promise, issues, and interpretations. Neuroimage, 80, 360–378. [PubMed: 23707587]

Jiang Y (2004). Resolving dual-task interference: an fMRI study. Neuroimage, 22(2), 748–754. [PubMed: 15193603]

Kucyi A, & Davis KD (2014). Dynamic functional connectivity of the default mode network tracks daydreaming. Neuroimage, 100, 471–480. [PubMed: 24973603]

Kucyi A, Hove MJ, Esterman M, Hutchison RM, & Valera EM (2017). Dynamic Brain Network Correlates of Spontaneous Fluctuations in Attention. Cereb Cortex, 27(3), 1831–1840. [PubMed: 26874182]

Kucyi A, Tambini A, Sadaghiani S, Keilholz S, & Cohen JR (2018). Spontaneous cognitive processes and the behavioral validation of time-varying brain connectivity. Network Neuroscience, 2(4), 397–417. [PubMed: 30465033]

Laumann TO, Snyder AZ, Mitra A, Gordon EM, Gratton C, Adeyemo B, … Petersen SE (2017). On the Stability of BOLD fMRI Correlations. Cereb Cortex, 27(10), 4719–4732. [PubMed: 27591147]

Mooneyham BW, Mrazek MD, Mrazek AJ, Mrazek KL, Phillips DT, & Schooler JW (2017). States of Mind: Characterizing the Neural Bases of Focus and Mind-wandering through Dynamic Functional Connectivity. Journal of Cognitive Neuroscience, 29(3), 495–506. [PubMed: 27779908]

Nijboer M, Borst J, van Rijn H, & Taatgen N (2014). Single-task fMRI overlap predicts concurrent multitasking interference. Neuroimage, 100, 60–74. [PubMed: 24911376]

Pruim RHR, Mennes M, Buitelaar JK, & Beckmann CF (2015). Evaluation of ICA-ROMA and alternative strategies for motion artifact removal in resting state fMRI. Neuroimage, 112, 278–287. [PubMed: 25770990]

Pruim RHR, Mennes M, van Rooij D, Llera A, Buitelaar JK, & Beckmann CF (2015). ICA-AROMA: A robust ICA-based strategy for removing motion artifacts from fMRI data. Neuroimage, 112, 267–277. [PubMed: 25770991]

Raichle ME (2015). The brain's default mode network. Annu Rev Neurosci, 38, 433–447. [PubMed: 25938726]

Schaefer A, Kong R, Gordon EM, Laumann TO, Zuo XN, Holmes AJ, … Yeo BTT (2018). Local-Global Parcellation of the Human Cerebral Cortex from Intrinsic Functional Connectivity MRI. Cereb Cortex, 28(9), 3095–3114. [PubMed: 28981612]

Seeley WW, Menon V, Schatzberg AF, Keller J, Glover GH, Kenna H, … Greicius MD (2007). Dissociable intrinsic connectivity networks for salience processing and executive control. J Neurosci, 27(9), 2349–2356. [PubMed: 17329432]

Shulman GL, Fiez JA, Buckner RL, Miezin FM, Raichle ME, & Peterson SE (1997). Common blood flow changes across visual tasks: II.: decreases in cerebral cortex. Journal of Cognitive Neuroscience, 9, 648–663. [PubMed: 23965122]

Silvia PJ, Winterstein BP, Willse JT, Barona CM, Cram JT, Hess KI, … Richard CA (2008). Assessing creativity with divergent thinking tasks: Exploring the reliability and validity of new subjective scoring methods. Psychology of Aesthetics, Creativity, and the Arts, 2(2), 68–85.

Smallwood J, & Schooler JW (2006). The restless mind. Psychol Bull, 132(6), 946–958. [PubMed: 17073528]

Smallwood J, & Schooler JW (2015). The science of mind wandering: empirically navigating the stream of consciousness. Annu Rev Psychol, 66, 487–518. [PubMed: 25293689]

Spreng RN, Mar RA, & Kim AS (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(3), 489–510. [PubMed: 18510452]

Spreng RN, Stevens WD, Chamberlain JP, Gilmore AW, & Schacter DL (2010). Default network activity, coupled with the frontoparietal control network, supports goal-directed cognition. Neuroimage, 53(1), 303–317. [PubMed: 20600998]

Stuss DT, Murphy KJ, Binns MA, & Alexander MP (2003). Staying on the job: the frontal lobes control individual performance variability. Brain, 126(Pt 11), 2363–2380. [PubMed: 12876148]

Szameitat AJ, Vanloo A, & Muller HJ (2016). Central as well as Peripheral Attentional Bottlenecks in Dual-Task Performance Activate Lateral Prefrontal Cortices. Front Hum Neurosci, 10, 119. [PubMed: 27014044]

Toro R, Fox PT, & Paus T (2008). Functional coactivation map of the human brain. Cereb Cortex, 18(11), 2553–2559. [PubMed: 18296434]

Vincent JL, Kahn I, Snyder AZ, Raichle ME, & Buckner RL (2008). Evidence for a frontoparietal control system revealed by intrinsic functional connectivity. J Neurophysiol, 100(6), 3328–3342. [PubMed: 18799601]

Wais PE, & Gazzaley A (2014). Distractibility during retrieval of long-term memory: domain-general interference, neural networks and increased susceptibility in normal aging. Front Psychol, 5, 280. [PubMed: 24778623]

Wang C, Ong JL, Patanaik A, Zhou J, & Chee MW (2016). Spontaneous eyelid closures link vigilance fluctuation with fMRI dynamic connectivity states. Proc Natl Acad Sci U S A, 113(34), 9653–9658. [PubMed: 27512040]
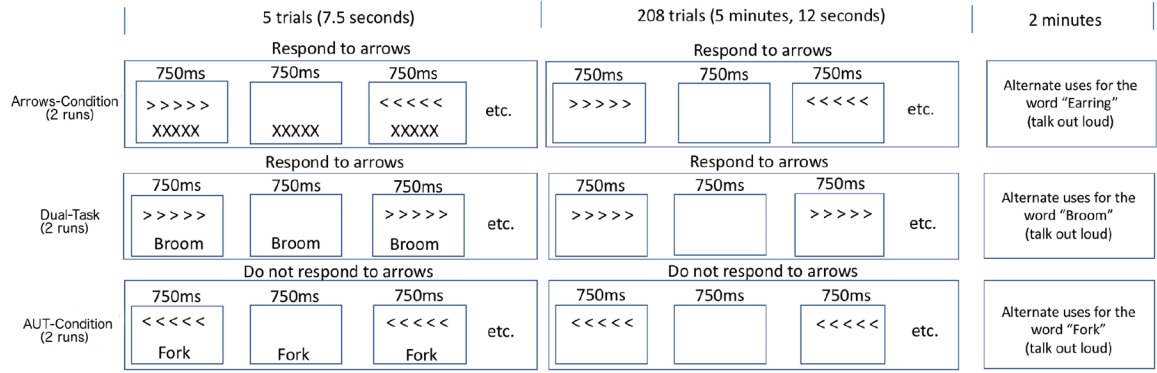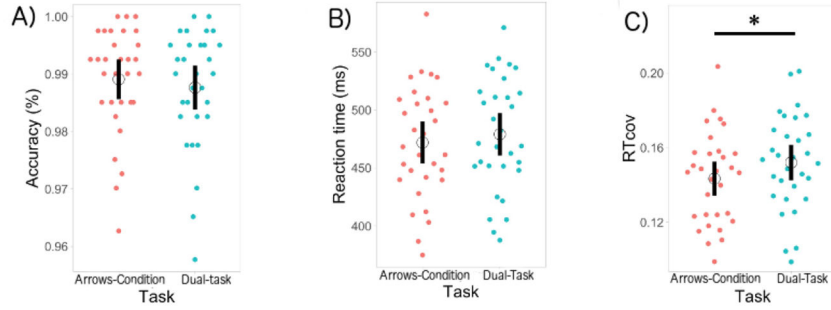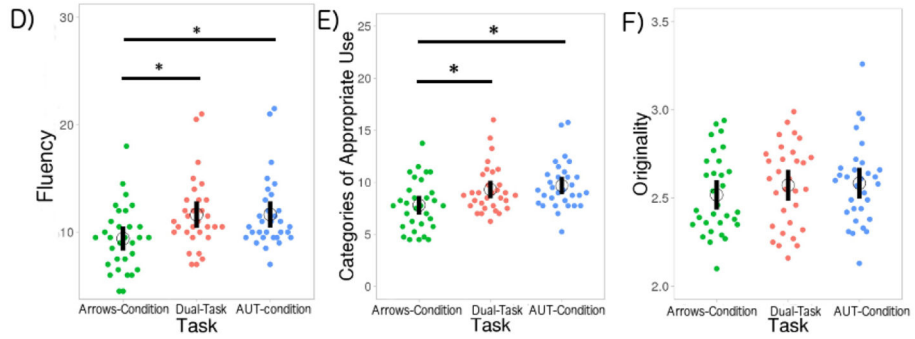
Figure 1:
Overview of the three conditions. The first phase of the three conditions lasted 7.5 seconds. In this phase, in the Dual-Task and AUT-condition, participants were shown the word for which they would have to list alternate uses later on whereas in the Arrows-condition, a string of "XXXXX" was shown instead. Arrows were presented for 750ms, pointing either left or right. A 750ms inter-trial interval separated each task trial. Participants were required to respond to the arrows in the Arrows-Condition and Dual-Task conditions but not in the AUT-condition. The second phase lasted 5 minutes and 12 seconds. In phase 2, arrows appeared on the screen as in phase 1, and again, participants responded to the arrows only in the Arrows-Condition and Dual-Task condition only. fMRI scanning was stopped following the completion of the second phase. The third phase lasted 2 minutes. In this phase, in the Arrows-Condition, Dual-Task and AUT-condition, participants were asked to verbally report alternate uses for a given word.
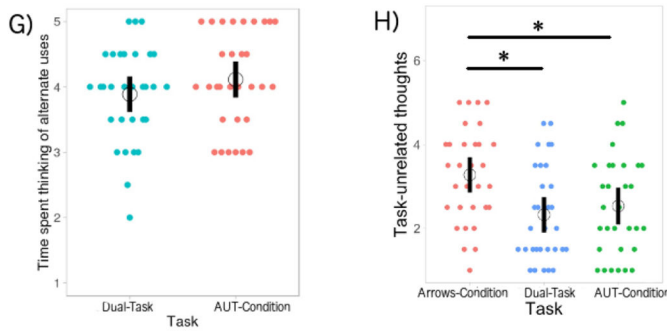
Figure 2:
This figure summarizes the behavioural results. a) Accuracy, b) mean reaction time (RT) and c) RTcov for the arrows task in the Arrows-Condition and the Dual-Task condition. D) Fluency, e) Categories of Appropriate Use and f) Originality ratings for the alternate uses task. G) Subjective estimates of time thinking of alternate uses. H) Subjective estimates of time spent having task-unrelated thoughts.
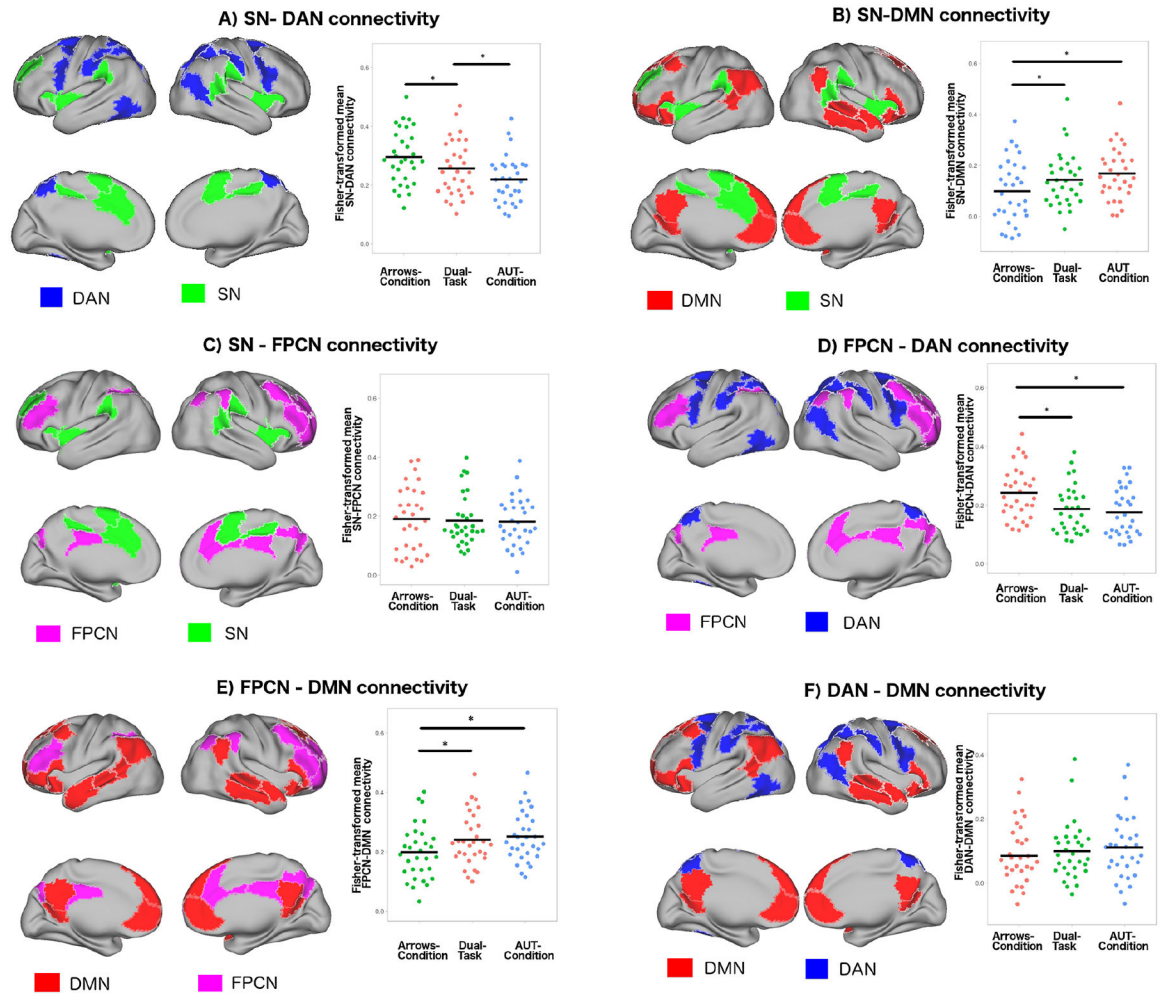
Figure 3:
This figure depicts task-related differences in the fisher-transformed average static connectivity values between a) salience network (SN) and Dorsal attention network (DAN), b) SN and default-mode network (DMN), c) SN and frontoparietal control network (FPCN), d) FPCN and DAN, e) FPCN and DMN and f) DAN and DMN. The brain pictures depict the regions of interest that were selected for analysis.
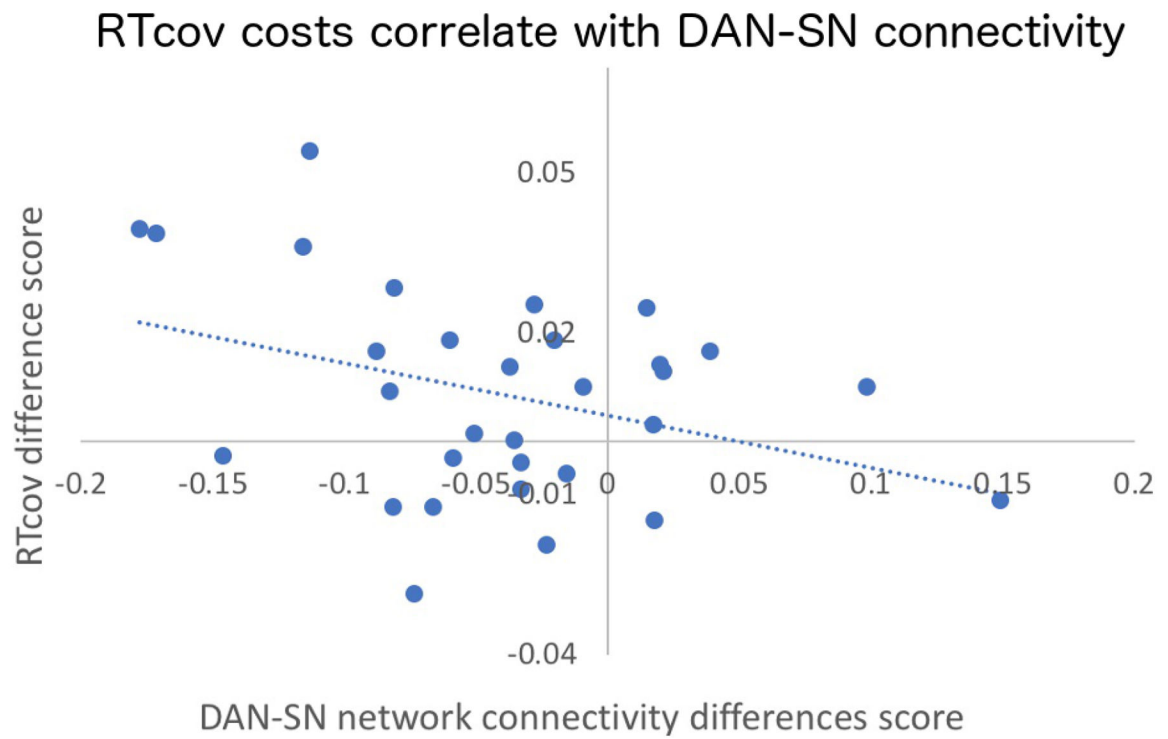
Figure 4:
Correlation between RTcov costs (RTcov in the Dual-Task condition minus the Arrows-condition) and DAN-SN connectivity differences scores (DAN-SN connectivity in the Dual-Task condition minus the Arrows-Condition).
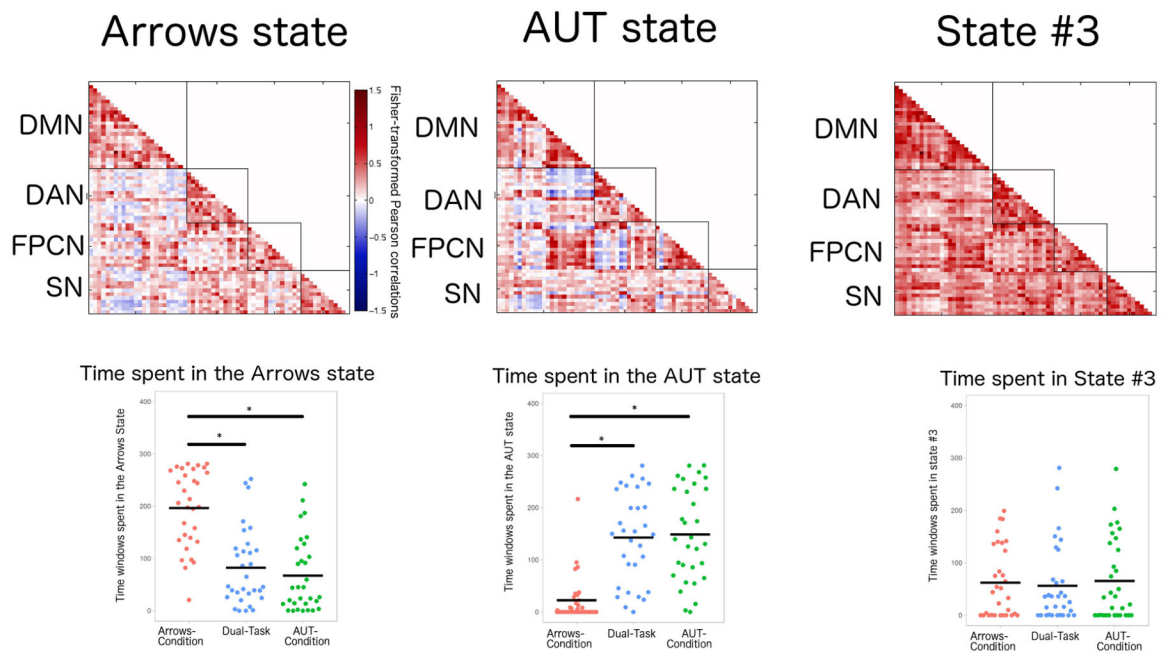
Figure 5:

This figure depicts the connectivity matrices associated with a) the Arrows State, b) the AUT State and c) State #3, as well as task-related differences in time spent in each state. The square boxes in the connectivity matrices delimit regions of interest associated with each network (DMN, DAN, FPCN and SN).

In the Dual-Task condition, time spent in the Arrows state is negatively correlated with subjective estimates of time spent thinking of alternate uses
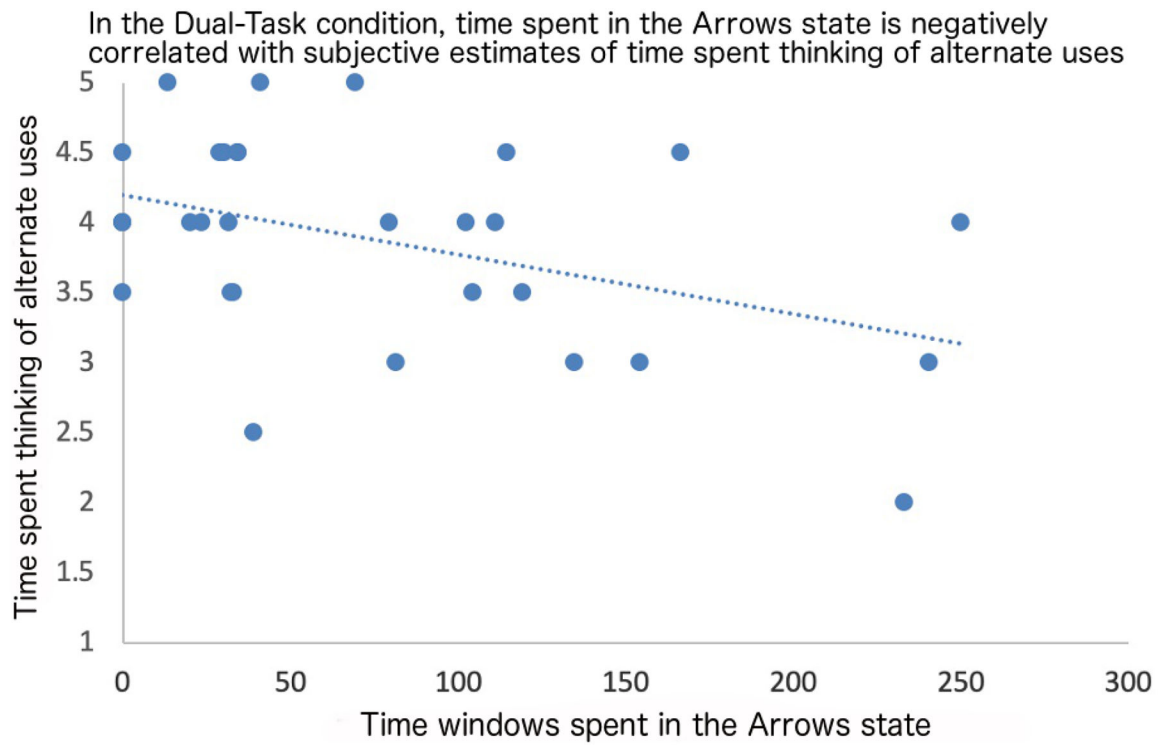
Figure 6:

This figure depicts the correlation between time spent in the Arrows state and subjective estimates of time spent thinking of the alternate uses task in the Dual-Task condition.

Table 1:

Descriptive statistics (means with standard deviation) for the behavioral data

	Arrows-Condition	**Dual-Task**	**AUT-condition**
Arrows Task			
Accuracy	0.99 (0.01)	0.99 (0.01)	N/A
Mean RT	471.87 (48.51)	479.07 (49.08)	N/A
RTcov	0.14 (0.02)	0.15 (0.03)	N/A
AUT			
Fluency	9.40 (3.01)	11.60 (3.33)	11.60 (3.29)
Categories of appropriate uses	7.81 (2.40)	9.31 (2.25)	9.69 (2.26)
Originality	2.52 (0.22)	2.57 (0.23)	2.58 (0.23)
Post-task subjective ratings			
Time spent thinking of the AUT	N/A	3.89 (0.73)	4.11 (0.74)
Task-unrelated thoughts	3.27 (1.12)	2.32 (1.13)	2.53 (1.18)

Note: AUT = Alternate uses task

Table 2:

Static connectivity (SD) for each condition

	Arrows-Condition	AUT-Condition	Dual-Task
SN - DAN	0.30 (0.09)	0.22 (0.08)	0.26 (0.09)
SN - DMN	0.10 (0.12)	0.17 (0.10)	0.14 (0.11)
SN - FPCN	0.19 (0.11)	0.18 (0.08)	0.18 (0.09)
FPCN - DAN	0.24 (0.09)	0.18 (0.08)	0.19 (0.08)
FPCN - DMN	0.20 (0.09)	0.25 (0.08)	0.24 (0.09)
DAN - DMN	0.09 (0.11)	0.11 (0.10)	0.10 (0.09)

Note: SN = Salience Network, DAN = Dorsal Attention Network, DMN = Default-Mode Network, FPCN = Frontoparietal Control Network, AUT = Alternate Uses Task

Table 3:

Average between-network connectivity for each time-varying connectivity state

	Arrows state	AUT state	State #3
DMN - DAN	0.04	0.05	0.29
DMN - FPCN	0.17	0.23	0.38
DMN - SN	0.04	0.12	0.34
DAN - FPCN	0.18	0.13	0.36
DAN - SN	0.24	0.19	0.41
FPCN - SN	0.13	0.14	0.35

Note: AUT = Alternate uses Task, DMN = Default-mode network, DAN = dorsal attention network, FPCN = frontoparietal control network, SN = salience network