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Timing Is Everything: Age Differences in the Cognitive Control Network Are Modulated by Time of Day

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Behavioral evidence suggests that the attention-based ability to regulate distraction varies across the day in synchrony with a circadian arousal rhythm that changes across the life span. Using functional magnetic resonance imaging (fMRI), we assessed whether neural activity in an attention control network also varies across the day and with behavioral markers. We tested older adults in the morning or afternoon and younger adults tested in the afternoon using a 1-back task with superimposed distractors, followed by an implicit test for the distractors. Behavioral results replicated earlier findings with older adults tested in the morning better able to ignore distraction than those tested in the afternoon. Imaging results showed that time of testing modulates task-related fMRI signals in older adults and that age differences were reduced when older adults are tested at peak times of day. In particular, older adults tested in the morning activated similar cognitive control regions to those activated by young adults (rostral prefrontal and superior parietal cortex), whereas older adults tested in the afternoon were reliably different; furthermore, the degree to which participants were able to activate the control regions listed above correlated with the ability to suppress distracting information.

Keywords: chronotype, aging, distraction, implicit memory, control network

There are well known circadian fluctuations in cognitive alertness (Blatter & Cajochen, 2007; Hasher, Zacks, & May, 1999b; Murray et al., 2009; Paradee, Rapport, Hanks, & Levy, 2005; Yoon, May, & Hasher, 1999), fluctuations measurable with paper-and-pencil-inventories that are highly correlated with physiological arousal (Horne & Ostberg, 1976; Roenneberg, Wirz-Justice, & Mellow, 2003; Zavada, Gordijn, Beersma, Daan, & Roenneberg, 2005). In addition, there are age and individual differences in alertness patterns, such that the majority of older adults tend to shift toward “morningness,” with younger adults falling into neutral and evening-type ranges of alertness. There is also a substantial behavioral literature showing a synchrony effect (Hornik & Tal, 2009; Lehmann, Marks, & Hanstock, 2013; May, Hasher,

Stoltzfuz, & Stoltzfus, 1993; May & Hasher, 1998; Rowe, Hasher, & Turcotte, 2009; Yang, Hasher, & Wilson, 2007), such that performance, particularly on tasks requiring attention control or suppression, are best performed at times of day that match versus mismatch arousal patterns (Goldstein, Hahn, Hasher, Wiprzycka, & Zelazo, 2007; Hahn et al., 2012; Hasher, Goldstein, & May, 2005; Intons-Peterson, Rocchi, West, McLellan, & Hackney, 1999; Lehmann et al., 2013; May & Hasher, 1998; May, 1999; Ramírez et al., 2006; Ramírez, García, & Valdez, 2012; Rowe et al., 2009; Yoon et al., 1999). Similar effects have also been demonstrated in animal studies that have reported Robust Age \times Synchrony interactions for arousal and memory (Winocur & Hasher, 1999, 2002). Despite a rich behavioral literature, the influence of circadian rhythms and time of testing has been largely unexplored in the neuroimaging literature, and what research there is has focused on young adults (e.g., Marek et al., 2010) showing time-of-day differences in the ability to regulate strong but incorrect responses in the orienting attentional network—the subdivision of the task-positive network that regulates where and when attention is directed in response to external cues (Schmidt et al., 2012). Although limited, these findings are suggestive for young adults, but an open and critical question is still the impact of different times of testing for older adults, whose behavioral data have shown substantially larger fluctuations, including in regulation of distraction, across the day than young adults’ data (e.g., Lustig, Hasher, & Tonev, 2001; May, 1999). We focus here on regulation of distraction because of its well-known time-of-day effects for older adults and because it has been shown to correlate with other cognitive functions including working memory capacity and fluid intelligence (Dempster, 1991, 1992; Hasher & Zacks, 1988; Lustig, Hasher, & Tonev, 2006).

To address the question of older adults’ distraction regulation, and the neural correlates of this ability across the day, we used

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functional magnetic resonance imaging (fMRI) and tested a group of morning-type elderly participants at an optimal time of day (~8:00 a.m.) and compared their performance on a simple 1-back task, with target information (pictures or words) superimposed by distraction, with that of younger and older participants tested at ~3:00 p.m., some of whose data had been previously collected (Campbell, Grady, Ng, & Hasher, 2012). We replicated behavioral data reported previously with a similar task (Rowe, Valderrama, Hasher, & Lenartowicz, 2006) and, it is critical to note, we reported differences in activity patterns across the day, with older adults tested in the morning having neural activity more similar to that of young adults than their age-peers tested in the afternoon. Insofar as the present task relied on an attention-control network engaged in tasks such as dual-task target detection (Geerligs, Saliassi, Maurits, Renken, & Lorist, 2014), implicit encoding of irrelevant face information during a working memory task, (Minamoto, Osaka, Engle, & Osaka, 2012), planning and execution of set shifting, and deploying visuospatial attention (Simard et al., 2011; Simpson et al., 2011; Spreng, Sepulcre, Turner, Stevens, & Schacter, 2013), these data suggested that our understanding of neural differences between young and older adults may be far from complete, particularly because few, if any, publications have indicated the time at which participants were tested.

Method

Participants

Participants included 17 younger and 16 older adults tested in the afternoon (1:00–5:00 PM, average starting time = 2:42 p.m.; data from 24 afternoon participants had previously been reported in Campbell et al., 2012), as well as 20 older adults tested in the morning (8:30–10:30 a.m., average starting time = 8:47 a.m.). One older participant from the morning group was excluded due to an incidental finding, and another due to awareness on the implicit task. Two younger adults were excluded from all analyses—one for not following the instructions for the critical 1-back task; the other reported awareness on the implicit task. The final *ns* were therefore: 16 younger adults (19–30 years; $M = 23.94$, $SD = 4.17$; 8 men) tested in the afternoon, 16 older adults tested in the afternoon (60–82 years; $M = 71.27$, $SD = 7.68$; 4 men), and 18 older adults tested in the morning (60–87 years; $M = 68.83$, $SD = 7.2$; 6 males). Participants were all right-handed, had normal or corrected-to-normal vision, and were cognitively normal according to the Mini Mental State Exam (Folstein, Folstein, & McHugh, 1975). Older adults in the morning ($M = 60.53$, $SD = 8.17$) and evening ($M = 63.67$, $SD = 10.81$) groups fall into the “moderately morning” chronotype and did not differ on the Morningness–Eveningness Questionnaire (MEQ), $p = .35$, but using two independent *t* tests, each was significantly different than younger adults ($M = 46.66$, $SD = 11.35$), $ps < .001$, whose mean score tended toward “eveningness” (Horne & Ostberg, 1976).

Procedure

The experimental design, materials, and procedure were all identical to those reported in Campbell et al. (2012), except that the new group of older adults was tested in the morning; new participants were also added to the two other groups. Briefly,

participants performed a series of tasks within the fMRI scanner. The order of tasks was as follows: (a) 1-back task on pictures with irrelevant words or nonwords (Run 1), (b) 7-min nonverbal Flanker task, which served as a filler task (unscanned), (c) implicit word-fragment-completion task (to test memory for the unattended words from the first 1-back task; unscanned), (d) 1-back task on letter stimuli with irrelevant pictures (Run 2), (e) 7-min resting-state scan with eyes closed (Run 3), and finally, (f) a second word-fragment completion task (to test memory for the attended words from the second 1-back task; unscanned). The picture 1-back task was always given first because this was our main measure of attention regulation (the ability to ignore superimposed, irrelevant words) and it included an implicit measure for memory for those words as behavioral markers for the failure to regulate distraction (see Rowe et al., 2006). Testing memory for the attended-words condition first could have alerted participants to a connection between successive tasks. To assess awareness of the connection between the fragment-completion task and the presence of distractors on the picture 1-back task, we also asked participants after the first fragment task if they had noticed a connection between the tasks thus far and if so, what they thought it was. Only one younger and one older adult were aware of the connection.

For the 1-back tasks, participants viewed a series of superimposed picture and letter stimuli (words and nonwords), with the pictures shown in red and the letters shown in black. Each stimulus pair was shown for 1,000 ms, followed by a blank screen for 500 ms. Across two separate runs, participants were asked to attend to either the pictures or the letters and to press a response key whenever the same stimulus (from the attended modality) appeared twice in a row. They were told to ignore stimuli from the unattended modality, as attention toward these stimuli would only worsen target task performance. One-back targets occurred every six trials on average and never coincided with targets for the word-fragment task. A block design was used, with the letter stimuli divided into word and nonword blocks. Thus, there were five different block types in total: fixation, ignore-words (attend pictures), ignore-nonwords (attend pictures), attend-words (ignore pictures), and attend-nonwords (ignore pictures). Each run began with 10 s of fixation, followed by eight task blocks of 24 s each, interleaved with eight fixation blocks of 14 s each. Each task block contained 16 trials of the same condition and thus, there were 64 trials per condition. Pictures were taken from Snodgrass and Vanderwart (1980) and superimposed with either random consonant strings or words (including 10 words in each task that would later serve as targets on a word-fragment-completion task).

All picture and word lists were counterbalanced, such that the pictures and words used on the attend-pictures 1-back (and corresponding fragment task) for one person would be used on the attend-letters 1-back for another person, and vice versa.

Memory for both the attended and unattended superimposed words was tested using word-fragment completion. Each test included 30 word fragments: 10 were target fragments that could be solved with words seen on the preceding 1-back task, 10 were control fragments which participants from another counterbalance condition would have seen, and 10 were easily solved fragments that served to maintain morale and to obscure the connection between the test and previous input task. Each fragment was shown in the center of the screen for 3,000 ms and participants

were told to respond aloud with the first solution that came to mind.

All fragments had multiple solutions in the language, but only one in the experiment. Separate baseline word-fragment-completion rates (the proportion of solved fragments from the unseen list) were determined for each age group and fragment task.

We used the arrow-flanker task as an unscanned filler between the initial priming and the word-fragment-completion task; briefly, participants were asked to respond only to the central chevron, which would be flanked by congruent (facing in the same direction) or incongruent chevrons. The “flanker effect” is obtained by subtracting reaction times (RTs) on congruent trials from incongruent trials, and the amount of slowing relative to the congruent trial is a measure of attentional failure (Eriksen & Eriksen, 1974). Only RTs from correct trials were included (all participants were close to ceiling, > 80% accurate), and a 2-SD trim was applied prior to analysis.

Functional MRI Data Acquisition

Participants were scanned using a Siemens Trio 3T scanner (Erlangen, Germany). Anatomical scans were acquired with a three-dimensional magnetization-prepared rapid acquisition with gradient echo (MP-RAGE) sequence (repetition time (TR) = 2 s, echo time (TE) = 2.63 ms, field of view (FOV) = 25.6 cm², 256 × 256 matrix, 160 slices of 1-mm thickness). Functional runs were acquired with an echo planar imaging (EPI) sequence, with 157 volumes for each the 1-back runs (TR = 2 s, TE = 30 ms, flip angle = 70°, FOV = 20 cm², 64 × 64 matrix, 30 slices of 5-mm thickness, no gap). Measures of pulse and respiration were obtained during the scan.

Preprocessing of the image data was performed with analysis of functional neuroimages (Cox, 1996). This included physiological motion correction, rigid motion correction, spatial normalization to Montreal Neurological Institute (MNI) space, and smoothing with an 8-mm Gaussian filter (the final voxel size was 4 × 4 × 4 mm). We also regressed out the white matter, cerebral spinal fluid, vasculature, and motion-time series from each voxel-time series (Campbell, Grigg, Saverino, Churchill, & Grady, 2013; Grady et al., 2010) and did not analyze the first 2 TRs from each block so we could have crisper transitions between conditions. As motion has been demonstrated to affect brain-activity measures, even after standard correction procedures (e.g., Power, Barnes, Snyder, Schlaggar, & Petersen, 2012), we followed a motion-scrubbing procedure described in Campbell et al., 2013. Briefly, this procedure uses a multivariate technique to identify outliers in both the motion-parameter estimates and fMRI signal itself. Where such outliers occurred (never more than 5% of the total volumes), we removed the fMRI volumes and replaced them with values interpolated with cubic splines. As reported by Campbell et al., (2013), this method has the advantage of suppressing spikes, yet keeping the length of the time course intact across subjects.

The image data were analyzed with partial least squares (PLS; for a detailed tutorial and review of PLS, see Krishnan, Williams, McIntosh, & Abdi, 2011; McIntosh, Bookstein, Haxby, & Grady, 1996; McIntosh, Chau, & Protzner, 2004), a multivariate analysis technique that identifies whole-brain patterns of covariance related to the experimental design (task

PLS) in a single step for multiple groups. This method is similar to principal component analysis (PCA), in that it identifies a set of principal components, or “latent variables” (LVs), which optimally capture the covariance between two sets of measurements (Friston, Frith, & Frackowiak, 1993). PLS uses singular value decomposition in a data-driven approach to reduce the complexity of the dataset into orthogonal LVs that attempt to explain the maximum amount of covariance between the task conditions and the blood-oxygen level dependent (BOLD) signal. As in PCA, the LVs are ordered in terms of variance explained, with the first LV often identifying networks held in common across groups or conditions, and subsequent LVs often demonstrating group differences.

In task PLS, each brain voxel has a weight, known as a salience, indicating how strongly that voxel contributes to the LV overall. The significance of each LV as a whole was determined with a permutation test (McIntosh et al., 1996) using 500 permutations. In addition, the reliability of each voxel’s contribution to a particular LV was tested by submitting all saliences to a bootstrap estimation of the standard errors (*SEs*; Efron, 1981), using 500 bootstraps. Peak voxels with a salience/*SE* ratio ≥ 3.0 ($p < .001$) are considered to be reliable (Sampson, Streissguth, Barr, & Bookstein, 1989). Clusters containing at least 10 reliable contiguous voxels were extracted, with a local maximum defined as the voxel with a salience/*SE* ratio higher than any other voxel in a 2-cm cube centered on that voxel (the minimum distance between peaks was 10 mm). Coordinates of these locations are reported in MNI standard coordinate space (Mazziotta et al., 2001). Because the extraction of the LVs and the corresponding brain images is done in a single step, no correction for multiple comparisons is required.

Finally, to obtain summary measures of each participant’s expression of each LV spatial pattern, we calculated brain scores by multiplying each voxel’s salience by the BOLD signal in the voxel, and summing over all brain voxels for each participant in each condition. These brain scores were then mean-centered (using the grand mean across all subjects and conditions) and confidence intervals (CIs; 95%) for the mean brain scores in each condition were calculated from the bootstrap. Following procedures used elsewhere (e.g., Garrett, Kovacevic, McIntosh, & Grady, 2010; Grady et al., 2010; Krishnan et al., 2011; McIntosh, 2004), conservative estimates of differences in activity between conditions and between groups were determined by a lack of overlap in these bootstrapped CIs. That is, nonoverlapping intervals between conditions within a group, or between groups within a condition, indicated a significant difference.

Results

Behavioral Results

Priming on the word-fragment-completion tasks was calculated for each participant as the difference between the proportion of target-word fragments correctly solved and the baseline for that list (using the baseline for each of the three groups). Mean baseline completion rates did not differ across age or time of testing (older a.m. = .10, older p.m. = .09, young p.m. = .13), $ps > .5$. One younger adult was aware of the connection between the first

1-back task and the first fragment task, and one older adult in the afternoon gave only two responses during the task, and thus, their priming scores for this task were not included in the analyses. Means and standard errors are shown in Figure 1. On the first fragment task, which tested priming for the superimposed, irrelevant words from the 1-back task on pictures, we initially conducted within-group t tests to assess whether priming was different from zero. Young adults showed no significant priming, $t(15) = 0$, whereas both groups of older adults did, $t(17) = 3.07$, $p = .007$, and $t(14) = 3.155$, $p = .007$ for the morning and afternoon groups, respectively. To test group differences, an ANOVA was conducted on the priming scores with a planned linear contrast. The overall ANOVA was significant, $F(2, 46) = 3.5$, $p = .038$, the linear contrast was also significant, $p = .017$, with priming increasing from nil in young adults to 7% in the morning group, and finally 11% in older adults tested in the afternoon. Our current results, therefore, agree with both the age and time-of-day-effect differences reported previously in a variant of this task (Rowe et al., 2006).

On the second fragment task, which tested priming for attended words from the 1-back task on letters, all groups showed significant priming, $ps < .05$, and there were no differences among groups, $F < 1$,

We also tested for age and time-of-day effects on the arrow-flanker task, another measure of distraction regulation. Accuracy for this task was close to ceiling (all groups scored above 80% for every condition). An ANOVA testing the difference in the “flanker effect” (where RT on congruent trials is subtracted from RT on incongruent trials) across groups was significant; $F(2, 47) = 4.62$, $p = .015$. As can be seen in Figure 1, young adults showed the smallest flanker effect, followed by the morning older and finally the afternoon older groups, and this was confirmed by a planned linear contrast, $p = .005$. Post hoc Bonferroni tests confirmed that once again, only the young and afternoon old groups differed, $p = .014$, showing that age differences in attention regulation and

inhibitory control are largest when older adults are tested at a nonoptimal time of day.

Functional MRI Results

The first LV from the task-PLS analysis ($p < .001$) accounted for 81.88% of the covariance in the data and differentiated the four task conditions (i.e., ignore words, ignore nonwords, attend words, attend nonwords) from fixation across all groups (see Figure 2). This LV showed classic activations in the task-positive and default networks that corresponded to task and fixation, respectively (Buckner, Andrews-Hanna, & Schacter, 2008; Fox et al., 2005; Raichle et al., 2001; Toro, Fox, & Paus, 2008). The task-positive network generally activates when participants engage in cognitively demanding tasks and includes such regions as the middle frontal gyri and parietal lobes. The default network, on the other hand, is activated by rest or self-reflection and includes medial prefrontal and posterior cingulate regions. This initial LV largely revealed no age or time-of-testing differences between groups across condition, as indexed by the overlapping CIs in the graph. One exception is that older adults tested in the afternoon activated the task-positive network *less*, and at least one default mode region (PCC) *more*, during the attend-words condition than both young adults and older adults tested in the morning, supporting the interpretation that, when comparing older and younger adults, testing older adults in the morning is a fairer comparison.

The second LV was also significant ($p < .022$), and explained 3.78% of the covariance in the data. This LV differentiated between groups on the tasks and neatly parallels the pattern of behavioral findings in the ignore-words condition, with a large difference between younger and older adults tested in the afternoon, with the older adults tested in the morning falling in between (see Figure 3). We find it important to note that older adults tested in the morning showed no statistical difference relative to younger adults in any of the conditions on this LV (i.e., CIs are overlapping

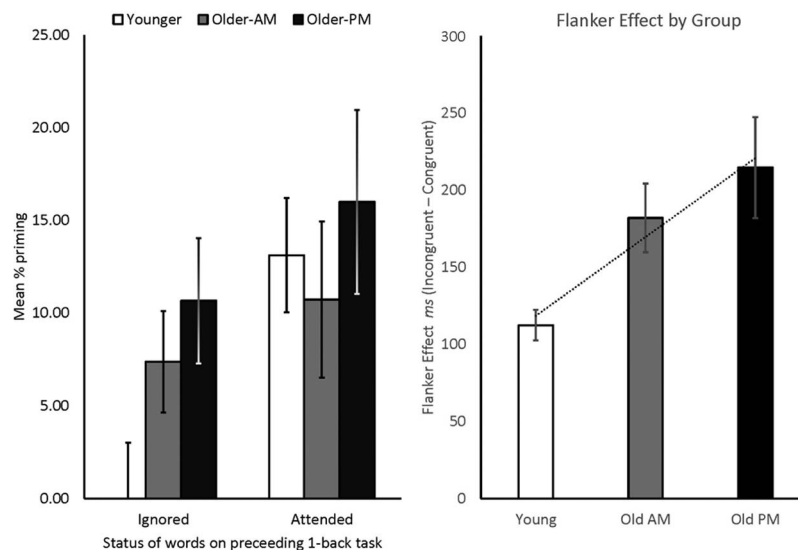


Figure 1. Behavioral results. Panel 1 shows mean percent priming as a function of age, time of day, and attention. Error bars represent ± 1 SEM. The second panel plots the flanker effect (difference in reaction times to congruent vs. incongruent trials) across group.

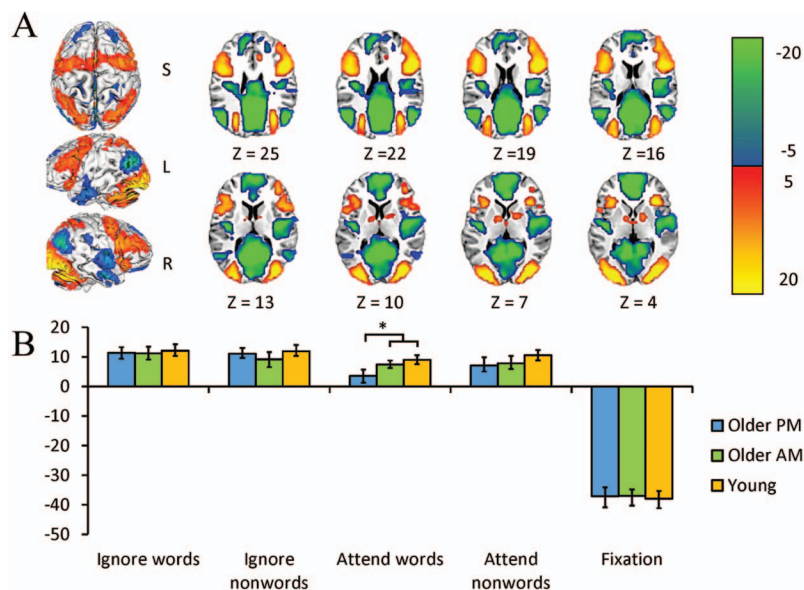


Figure 2. Results from the partial least squares (task-PLS) shown on a high resolution MNI152 canonical brain axial image. The pattern identified by this latent variable (LV) in (a) shows areas that all participants activated relative to fixation (warm colors) or where there was more activity during fixation (cool colors). The graph in (b) shows the mean-centered mean brain scores for each group on this LV (error bars represent the 95% CIs). Positive brain scores during the tasks correspond to more activity in warm-colored areas relative to overall mean activity (0 in the graph) and negative brain scores are associated with more activity during fixation (cool colors). A bootstrap ratio threshold of 5.0 was used to form the brain image in (a).

for these two groups). Younger adults along with older adults who were tested in the morning activated a set of regions (shown in warm colors in Figure 3) during the ignore words and ignore nonwords conditions (indicated by the positive brain scores on the graph), whereas these same regions were not activated by older adults tested in the afternoon (their confidence limits cross zero, indicating no difference from mean activity). These regions included the middle frontal gyri and parietal regions bilaterally (Figure 3A). These regions are part of the control network delineated by Vincent, Kahn, Snyder, Raichle, & Buckner, (2008), which is thought to underlie cognitive control. The pattern of activity seen here suggests that young adults are most able to access these control regions, and the age effect is partially mediated by time of testing. To test this pattern of brain activity for linear contrasts, we extracted the brain-scores for each individual by group and condition for the ignore-words and ignore-nonword conditions. In the ignore words condition, which requires suppression of a prepotent reading response, the linear trend was significant at $p = .003$, indicating an increasing engagement of cognitive control areas from afternoon older adults to morning older adults, and with the largest increase in young adults, to support ignoring or suppressing the distracting material. The linear effect was not significant in the ignore-nonword condition.

In the ignore-picture conditions, in which attention was directed to the words or nonwords, brain activity in the older adults tested in the afternoon differed from both of the other groups, showing robust increases of activity in a number of regions, including left inferior frontal cortex (shown in cool colors in Figure 3). Older adults tested in the morning also showed this activity, but to a lesser extent than afternoon-tested age mates. The left inferior

frontal region is commonly reported in language-processing tasks, including motor planning in anticipation of speech, subvocalization, learning new words, and encoding during speech production (Szenkovits, Peelle, Norris, & Davis, 2012; e.g., Veroude, Norris, Shumskaya, Gullberg, & Indefrey, 2010), suggesting that older adults tested in the afternoon, and to a lesser extent, older adults tested in the morning, were attending far more to the language component of the task than young adults. More activity in this region suggests that older adults, particularly when tested in the afternoon, tend to preferentially attend to word or word-like stimuli, despite their being irrelevant to the task. More activity in the afternoon older group during the ignore-picture conditions also was seen in the right PCC, left Rolandic operculum, and the middle occipital gyrus (cool-colored regions in Figure 3). The PCC has been implicated in relating encoded information to prior knowledge (e.g., Maguire, Frith, & Morris, 1999), suggesting that older adults in the afternoon were less able to prevent themselves from encoding information, or perhaps found the word-stimuli more captivating than the other two groups. We tested for a linear effect in this activity, as described above. This linear effect was significant, such that there was increased activation in the older adults tested in the afternoon during the attend-letter conditions, with less activation in the morning older adults, and no significant activation in the younger adults (both $ps < 0.001$, Figure 3).

Finally, to test for brain-behavior relationships, we correlated the extracted brain scores from the ignore-words condition with priming for distraction (see Figure 4). Under the assumption that engagement of frontoparietal control regions during the ignore-words condition would lead to less priming regardless of age or time of testing, we collapsed across groups and tested the overall

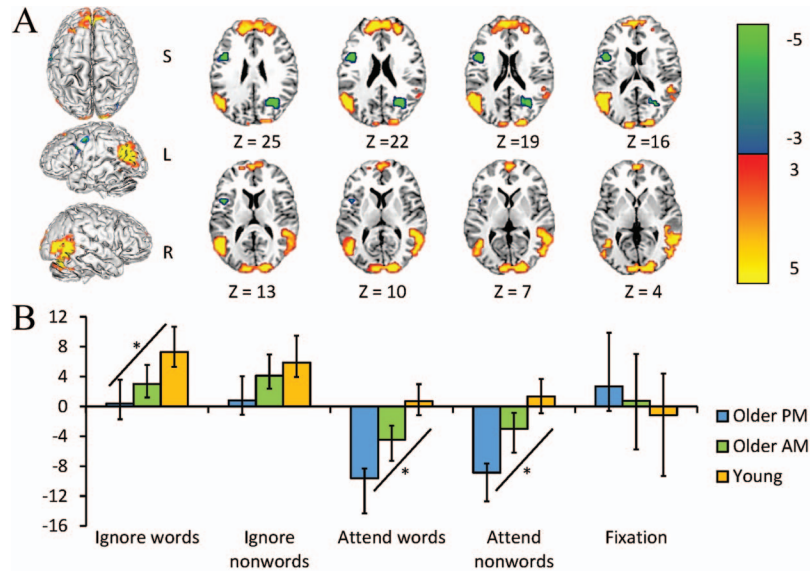


Figure 3. Results from the second latent variable (LV) shown on a high-resolution MNI152 axial image. The pattern identified by this LV in (a) shows areas with increased activity primarily during the ignore-words and ignore-nonwords conditions (warm colors). The graph in (b) shows the mean-centered mean brain scores for both groups on this LV (error bars represent the 95% CIs). Group differences are indicated by a lack of overlap in the CIs; for example, during the ignore-words condition, younger adults showed more activity than older adults tested in the afternoon, but activity did not differ between younger adults and older adults tested in the morning. A bootstrap ratio threshold of 3.0 was used to form the brain image in (a).

correlation. This correlation was significant, $r = -0.29$, $p = .047$, suggesting that greater engagement of the regions that regulate cognitive control was associated with less priming for the distracting words.

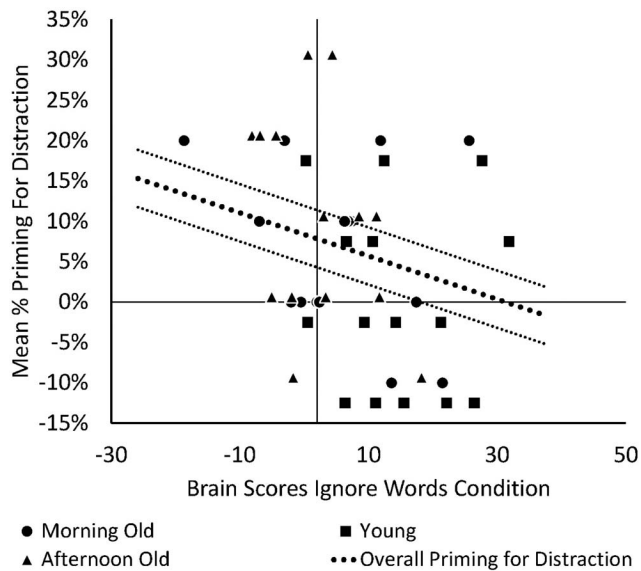


Figure 4. Brain-behavior correlation between priming for distraction and brain scores on the ignore-words condition. The correlation is $-.29$, $p = .047$, and is collapsed across groups.

Discussion

The current research demonstrated that when older adults are tested at their optimal time of day (morning), they rely on a similar set of neural regions underlying attention control in young adults, a region that correlates with improved ability to resist distraction. Older adults tested in the afternoon during their off-peak time of day showed both behavioral *and* neural decrements, as they were less able to resist distraction and to draw on the appropriate brain regions than young adults tested in the afternoon or age mates tested in the morning. Our research is consistent with previously established behavioral effects showing that, at synchrony or a time of day that matches circadian arousal patterns, older adults are able to resist distraction (Hasher et al., 2005; Rowe et al., 2006; Schmidt, Collette, Cajochen, & Peigneux, 2007), and it is crucial to note that, for the first time, we demonstrated that to do so, they activate a set of attentional control regions also recruited by younger adults.

The cognitive control network, which includes lateral and rostral prefrontal cortices and the inferior parietal lobules, may be a master “switch,” controlling access to the default and the dorsal attention networks (e.g., Gao & Lin, 2012). Recent work has suggested that not only is the control network interposed between the dorsal attention and default networks (Vincent et al., 2008), but it functionally modulates the relationship between them during tasks (Spreng, Stevens, Chamberlain, Gilmore, & Schacter, 2010), and at rest, is affected by endogenous levels of dopamine (Dang, O’Neil, & Jagust, 2012).

The idea that older adults have difficulty regulating activity in control regions, and by implication in modulating a putative net-

work “switch,” agrees with other literature suggesting that this group also has difficulty modulating functional connections between various regions comprising both task-positive and default networks (Grady et al., 2010; Lustig et al., 2003; Persson, Lustig, Nelson, & Reuter-Lorenz, 2007). There is also evidence that older adults may have difficulty suppressing the default network when on task, suggesting that they may be more prone to interference from mind-wandering, or reflecting on autobiographical memories during an experiment (Grady, Springer, Hongwanishkul, McIntosh, & Winocur, 2006; Park, Polk, Hebrank, & Jenkins, 2010). The current results suggest that time of testing may impact older adults’ ability to effectively modulate these networks.

Our results may also be interpreted in light of “CRUNCH” (compensation-related utilization of neural circuits hypothesis); older adults recruit more resources at lower loads than younger adults, but then plateau or fall off when loads get higher (whereas younger adults can increase activity at higher loads; Reuter-Lorenz & Cappell, 2008). Our results suggest that older adults in the afternoon experience higher load and have already plateaued, whereas those in the morning can still increase activity like young adults.

Hasher et al., (2005) observed that failing to take time of testing and chronotype (i.e., preferred time of day as measured by the MEQ or similar instrument) into account when studying age differences might bias results. In short, some of the variance in age differences reported in the literature could in fact reflect time-of-day differences whenever testing times are shifted away from early morning, the times at which most older adults are at a peak arousal. The current results also indicate that there are differences in brain activity across the day for older adults that match behavioral differences in an attention-control task. Insofar as attention regulation underpins a wide variety of other cognitive tasks (e.g.,

Dempster, 1991; Hasher et al., 1999; Lindenberger & Mayr, 2014; Lustig, Hasher, & Zacks, 2007), these findings are particularly important. Because few neuroimaging studies report time of testing, it is difficult to know to what degree age differences in such studies are associated with time-of-testing effects, and to what degree these differences influence the conclusions from such studies. Given the accumulation of evidence that time of testing can modulate age-related differences, this information should at the least be routinely reported.

We do not have a fully crossed design, in that young adults were not tested in the morning, in part because our central interest was in aging and patterns across the day, but also because time-of-testing differences for young adults tend to be smaller than for older adults (see, e.g., Winocur & Hasher, 1999; Yoon et al., 1999). We note that, because our young adults were tested in the afternoon at either a neutral or even optimal time, our results are biased against finding the lack of difference we observed between older adults and young adults tested in the morning. Finally, although we did not include measures of circadian variation beyond the MEQ, the MEQ nevertheless correlates strongly with circadian fluctuations in core body temperature; alertness is, therefore, an excellent proxy measure of circadian type in humans (Bailey & Heitkemper, 2001; Horne & Ostberg, 1976). That said, future work may need to include measures of sleep activity, including sleep diaries and actigraphy.

Neuroimaging results from this study suggest that brain activity for older adults varies substantially across the day, with greater engagement of attentional control areas in the morning than in the afternoon. Further, these differences in brain recruitment accompany behavioral differences seen across the day. Although it is currently unknown what is true for young adults, these data at least suggest the importance of reporting or controlling for the time at

Table 1
Brain Areas Showing an Age and Time-of-Day Difference Across Conditions From LV2

Region	Hemisphere	X (mm)	Y (mm)	Z (mm)	BSR
Ignore nonwords/words > Attend nonwords/words					
Middle temporal gyrus	L	-52	-60	16	7.08
Fusiform gyrus	R	32	-60	-16	6.36
Superior frontal gyrus	L	-4	40	44	6.06
Superior occipital gyrus	R	20	-92	16	6.01
Medial frontal gyrus	L	-8	52	24	5.49
Inferior temporal gyrus	R	56	-52	0	5.48
SMA	R	8	8	60	4.80
Middle frontal gyrus	R	24	44	24	4.62
Fusiform gyrus	L	-24	-68	-16	4.49
Cerebellum	L	-20	-52	-24	4.38
Superior parietal lobule	R	32	-48	56	4.37
Cerebellum	R	28	-76	-36	4.30
Posterior cingulate cortex	L	-4	-52	24	4.18
Precuneus	L	-4	-52	40	4.16
SMA	R	12	-12	64	4.11
Inferior temporal gyrus	L	-52	-8	-24	3.68
Middle frontal gyrus	L	-16	8	64	3.55
Ignore nonwords/words < Attend nonwords/words					
Rolandic operculum	L	-44	4	16	-5.70
Posterior cingulate cortex	R	28	-60	20	-5.65
Middle occipital gyrus	L	-28	-60	32	-4.45

Note. BSR (bootstrapped ratios) can be used to estimate the contribution of each cluster to the latent variable (LV). X = right/left; Y = anterior/posterior; Z = superior/inferior; SMA = Supplementary Motor Area.

which testing occurs, because conclusions about brain activity may be partly tied to time of testing, rather than to age. In summary, our results lend further credence to the extant behavioral work demonstrating that age-related decrements in cognitive control can be modulated by time of testing and chronotype, and establish for the first time that these effects extend to BOLD activity in fMRI. Finally, we emphasize that ignoring the time of day when testing older adults on some tasks may create an inaccurate picture of age differences in brain function.

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