

Sustained and Transient Processes in Event-based Prospective Memory in Adolescence and Adulthood

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Abstract

■ Prospective memory (PM) refers to the cognitive processes associated with remembering to perform an intended action after a delay. Varying the salience of PM cues while keeping the intended response constant, we investigated the extent to which participants relied on strategic monitoring, through sustained, top-down control, or on spontaneous retrieval via transient bottom-up processes. There is mixed evidence regarding developmental improvements in event-based PM performance after the age of 13 years. We compared PM performance and associated sustained and transient neural correlates in 28 typically developing adolescents (12–17 years old) and 19 adults (23–30 years old). Lower PM cue salience associated with slower ongoing task (OT) RTs, reflected by increased μ ex-Gaussian parameter, and sustained increases in frontoparietal

activation during OT blocks, both thought to reflect greater proactive control supporting cue monitoring. Behavioral and neural correlates of PM trials were not specifically modulated by cue salience, revealing little difference in reactive control between conditions. The effect of cue salience was similar across age groups, suggesting that adolescents are able to adapt proactive control engagement to PM task demands. Exploratory analyses showed that younger, but not older, adolescents were less accurate and slower in PM trials relative to OT trials than adults and showed greater transient activation in PM trials in an occipito-temporal cluster. These results provide evidence of both mature and still maturing aspects of cognitive processes associated with implementation of an intention after a delay during early adolescence. ■

INTRODUCTION

Prospective memory (PM) enables the execution of intended actions after a delay, for example, remembering to respond to an email after reading this paper (Meacham & Singer, 1977). Event-based PM refers to instances in which the action needs to be performed in response to a cue (event) in the environment, such as remembering to send the email “when you see your laptop” (Einstein, Holland, McDaniel, & Guynn, 1992). An event-based laboratory task typically embeds a PM task, in which participants are instructed to do a different action in response to a target cue, in an ongoing task (OT), which already requires a certain response to stimuli. Event PM can be split into two components: cue identification (e.g., the email icon on your computer) and intention retrieval (e.g., what to do in response to the cue—write and send email; Simons, Schölvink, Gilbert, Frith, & Burgess, 2006).

PM performance is influenced by the degree to which several task factors rely on more or less top-down executive control processes, as has been proposed by the multiprocess framework (McDaniel & Einstein, 2000), the preparatory attentional and memory (PAM) processes model (Smith, 2003), and, more recently, the Dual Mechanisms of Control (DMC) framework (Braver, 2012). The PAM theory posits that intention retrieval is only possible with nonautomatic monitoring of the PM cue (Smith, 2003). In contrast,

according to the multiprocess framework (McDaniel & Einstein, 2000), PM is supported by both strategic monitoring, which includes top-down sustained processes of intention maintenance and monitoring to detect a PM cue (McDaniel & Einstein, 2000), and spontaneous retrieval, associated with more transient bottom-up processes in which intentions “pop to mind” (Scullin, McDaniel, & Shelton, 2013; McDaniel & Einstein, 2007). Scullin and colleagues (2013) have proposed an extension, the dynamic multiprocess framework, whereby strategic monitoring and spontaneous retrieval could be both recruited in the same PM task, but at different times and/or in distinct contexts. The extent to which individuals rely on strategic monitoring or spontaneous retrieval depends on (1) characteristics of PM cues, including salience (how perceptually distinct PM cues are), valence, or focality (whether PM cue features are also the focus of the OT); (2) characteristics of the task, including cognitive load and importance; and (3) characteristics of the individual, such as cognitive capacity and personality traits (Cona, Scarpazza, Sartori, Moscovitch, & Bisiacchi, 2015; Einstein et al., 2005).

The DMC framework (Braver, 2012) separates proactive and reactive dimensions of cognitive control, which are associated with sustained and transient activity in the frontoparietal and salience networks, respectively (Jiang, Beck, Heller, & Egner, 2015; Braver, 2012). Mapping these aspects of cognitive control to PM processes may generate predictions at the brain level and lead to improved understanding of the cognitive processes supporting PM

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(McDaniel, LaMontagne, Beck, Scullin, & Braver, 2013). Proactive control supports the cognitively demanding active maintenance of goals in working memory and attending to the environment (Koslov, Mukerji, Hedgpeth, & Lewis-Peacock, 2019; Braver, 2012). While it is resource consuming, proactive engagement of preparatory processes would allow monitoring of the environment to detect PM cues that are nonsalient or less important (Einstein et al., 2005; Smith, 2003; McDaniel & Einstein, 2000). Reactive control would match with the less demanding retrieval of the intention from episodic memory (Koslov et al., 2019).

Salient PM cues facilitate performance (Mahy, Moses, & Kliegel, 2014; Kliegel et al., 2013; Altgassen, Phillips, Henry, Rendell, & Kliegel, 2010; Smith, Hunt, McVay, & McConnell, 2007; Einstein et al., 2005; Brandimonte & Passolunghi, 1994), reducing monitoring demands by encouraging spontaneous, automatic retrieval (Mahy et al., 2014), which does not load as much on cognitive demands and relies on reactive control triggered by the cue. The first aim of this study was to investigate the effects of manipulating cue salience on strategic monitoring, mapped onto proactive and reactive cognitive control processes (McDaniel et al., 2013; Braver, 2012), and how this relates to the facilitative effect of cue salience on performance.

PM in Adolescence

Age-related differences are apparent in PM performance across the lifespan. Most studies to date have focused on improvements in childhood and impairments in aging. Cross-sectional studies have found evidence of improvement in performance until the age of 13–14 years, when performance appears to level off through early adulthood and later worsens in older adulthood (Kliegel, Mackinlay, & Jäger, 2008; Zöllig et al., 2007; Zimmermann & Meier, 2006). By the age of 4 years, PM capacity is evident (Kvavilashvili, Messer, & Ebdon, 2001) and continues to increase during preschool years (Mahy et al., 2014; Ford, Driscoll, Shum, & Macaulay, 2012; Kliegel et al., 2008; Guajardo & Best, 2000). In middle childhood, performance continues to improve (Voigt et al., 2014; Smith, Bayen, & Martin, 2010; Mackinlay, Kliegel, & Mäntylä, 2009; Kerns, 2000). Not many studies have focused on adolescent and young adulthood samples, however, and the evidence regarding continued development in this age group is mixed. Some studies show further improvement of PM performance in adolescence (from 12 to 16 years old) compared to adults (Altgassen, Kretschmer, & Schnitzspahn, 2017; Bowman, Cutmore, & Shum, 2015; Altgassen, Vetter, Phillips, Akgün, & Kliegel, 2014; Wang et al., 2011; Zöllig et al., 2007; Wang, Kliegel, Yang, & Liu, 2006), particularly when PM cues are not focal to the processes involved in the OT. In contrast, some studies do not find strong evidence for development after early adolescence (Bowman et al., 2015; Wang et al., 2011; Zimmermann & Meier, 2006; Ward, Shum, McKinlay, Baker-Tweney, & Wallace, 2005), with adolescents (over

13 years old) and adults performing similarly better than children, and later on, quite stable performance in young to middle adulthood (Kliegel et al., 2008).

Other executive control processes that could contribute to PM, such as working memory and inhibitory control, develop extensively during childhood and adolescence (Zanolie & Crone, 2018; Humphrey & Dumontheil, 2016; Munakata, Snyder, & Chatham, 2012; Best & Miller, 2010). Performance in prospective tasks that are particularly demanding might therefore be specifically impaired in adolescents, compared to adults (Bowman et al., 2015; Altgassen et al., 2014; Mahy et al., 2014; Kliegel et al., 2013). For example, adolescents have poorer PM performance than adults on tasks that use nonfocal cues (Altgassen et al., 2014; Wang et al., 2011; Zöllig et al., 2007). In contrast, manipulation of cue salience to lessen cognitive demands can reduce age-related differences as has been shown in children (Kliegel et al., 2013) and also older adults (Altgassen et al., 2010).

Specifically, developmental differences in PM performance might be related to an immature ability to sustain cognitive control in adolescence, as it has been suggested that adolescent participants rely more on reactive strategies than do adults in some contexts (Munakata et al., 2012; Andrews-Hanna et al., 2011), although see Magis-Weinberg, Custers, and Dumontheil (2019) for evidence of flexible reactive and proactive control engagement in adolescence. This imbalance might impact the ability to monitor for PM cues, as salient and nonsalient cues may recruit reactive and proactive control differentially and particularly challenge developing adolescent cognitive resources. Another driver of developmental differences may be orientation toward the future, which matures during adolescence (Steinberg et al., 2009) and has been shown to enhance PM function in adolescents (Altgassen et al., 2017) and adults (Altgassen et al., 2014).

The second aim of this study was therefore to directly test whether adolescents differed from adults in their ability to flexibly recruit proactive and reactive control of PM as a function of cue salience and whether age-related differences may be accounted for by developmental differences in executive functioning or future orienting.

Neural Bases of PM

In adults, PM performance is robustly associated with a series of frontoparietal regions (for a review, see Cona et al., 2015; Burgess, Gonen-Yaacovi, & Volle, 2011). The rostrolateral pFC (RLPFC), approximating Brodmann's area (BA) 10, has been the main region implicated in intention maintenance (Burgess, Dumontheil, & Gilbert, 2007; Gilbert et al., 2006). The dorsolateral pFC (DLPFC) and precuneus have been associated with monitoring (McDaniel et al., 2013; Kalpouzos, Eriksson, Sjölie, Molin, & Nyberg, 2010), whereas more ventral frontoparietal and temporo-parietal networks have been related to PM cue attention capture and intention retrieval (Beck, Ruge, Walser, &

Goschke, 2014; McDaniel et al., 2013; Kalpouzos et al., 2010). Cue detection and intention retrieval have been associated with transient activity in ACC, posterior cingulate cortex, and temporal cortex (Beck et al., 2014; Gonneaud et al., 2014; Gilbert, Armbruster, & Panagiotidi, 2012; Rusted, Ruest, & Gray, 2011; Gilbert et al., 2006). The anterior insula (AI) is frequently associated with PM, with reports of both sustained and transient activation (Beck et al., 2014; Rea et al., 2011; Gilbert, Gollwitzer, Cohen, Oettingen, & Burgess, 2009; Simons et al., 2006), suggesting a role in cue monitoring as well as increasing cue salience (Cona et al., 2015).

A few studies using electrophysiology across the life span report differences with age in behavioral measures of PM and differences in neural activity measured through EEG between children, adolescents, and adults (Mattli, Zöllig, & West, 2011; Zöllig et al., 2007). ERPs generated in PM error trials have different sources in children and adolescents compared to adults. This suggests that various processes may have contributed to PM errors in younger participants (Mattli et al., 2011; Zöllig et al., 2007). Bowman and colleagues (2015) described development of two key PM ERP components (N300 and parietal positivity) across the whole range of adolescence (age: 12–19 years) in an OT of lexical decision with PM targets cued by different colored stimuli. They did not find age differences in N300 amplitude, but the parietal positivity was higher for the youngest (12–13 years old) compared to the oldest (18–19 years old) adolescent group, suggesting that cognitive processes associated with parietal positivity, such as general cognitive control capacities and working memory, are still developing.

fMRI neural correlates of PM function in adolescence remain insufficiently investigated (Dumontheil, 2014). However, studies investigating other aspects of cognitive control related to PM, such as abstract processing, integration, and coordination of information, have shown protracted development of their neural correlates in the RLPFC and parietal cortex during adolescence (Dumontheil, 2014; Dumontheil, Burgess, & Blakemore, 2008). This led us to hypothesize that adolescents would show poorer PM performance and associated differences in brain activity compared to adults. As for the behavioral measures, we further investigated whether developmental differences in PM may be related to developmental differences in executive function, using tasks previously shown to be sensitive to development during adolescence (digit span task for working memory, go/no-go task for inhibitory control).

This Study

Here, we adapted an event-based PM paradigm designed by Simons et al. (2006) to focus on cue identification. In this version of the task, we kept intention retrieval demands constant but manipulated cue salience, which is thought to modulate the degree of strategic, proactive monitoring, to investigate proactive and reactive processes in PM. The

DMC framework ties behavioral strategic monitoring with neural traces of proactive sustained cognitive control processes and automatic retrieval to reactive transient cognitive control. Participants performed an OT in which they indicated whether a triangle was to the left or right of another shape. Infrequent PM trials required pressing a different key if the shapes were the same color (salient cue condition) or if they were a chess knight's move apart (nonsalient cue condition). Our aims were to (1) investigate the effects of manipulating the salience of the cue on strategic monitoring and recruitment of proactive versus reactive control and (2) test whether adolescents differed from adults in behavioral and neural measures of PM and in their ability to flexibly recruit proactive and reactive control as a function of cue salience. Behavioral data were analyzed with a distribution modeling technique using ex-Gaussian functions, which has been used to characterize sustained and transient PM-induced cost effects (Ball & Brewer, 2018; Loft, Bowden, Ball, & Brewer, 2014; Abney, McBride, & Petrella, 2013). A mixed block–event fMRI design allowed us to investigate sustained and transient changes in BOLD signal associated with intention maintenance across the task block and PM trial execution, respectively (Magis-Weinberg et al., 2019).

We predicted that nonsalient PM cues would be associated with worse PM performance than salient cues (McDaniel & Einstein, 2000). In the neuroimaging data, we expected activations associated with PM in the RLPFC, DLPFC, and parietal cortex in adults (in line with Simons et al., 2006), and modulation of sustained and transient activity by cue salience, with greater sustained activation in the low-cue-salience condition, associated with greater proactive monitoring, and reversely greater transient activation during PM trials in the high-cue-salience condition, reflecting reactive control and bottom–up target detection processes. We predicted age-related differences in PM performance, with better performance in adulthood than adolescence. We explored to what extent age group differences in ex-Gaussian parameters related to overall RT (μ parameter), variability (σ parameter), and abnormally slow responses (τ parameter) contributed to RT interference costs associated with maintaining an intention. We explored whether adolescents exhibited different patterns of sustained and transient activation. We expected adolescents may show greater engagement of reactive control than adults, reflected in greater transient activation in PM trials. Adults were further expected to show greater differences in proactive control as a function of cue salience, which would reflect greater flexibility in proactive control engagement as a function of task demands. Finally, we tested whether laboratory-based behavioral and neural indices of PM associated with “real-life” subjective reports of PM and retrospective memory (Smith, Del Sala, Logie, & Maylor, 2000) and executive function failures (Buchanan et al., 2010) and whether neural and behavioral developmental differences in PM could be accounted for by developmental differences in executive functioning or future thinking.

METHODS

Participants

Nineteen adults (nine women, 22–30 years old, $M \pm SD = 27.1 \pm 1.9$ years) and 28 adolescents (15 girls, 12–17 years old, $M = 14.6 \pm 1.4$ years) participated in the study. Data from two additional adolescents were not included in the analyses as they had fewer than three correct PM trials, and data from one additional adult participant were discarded because of technical problems with stimuli presentation during scanning. Participants did not have any developmental or neurological disorders and were recruited through advertising, social media, word of mouth, and local participant volunteer databases. Participants were reimbursed £20 and their travel expenses for taking part in the study. This study was approved by the University College London Research Ethics Committee. Consent was obtained according to the Declaration of Helsinki; adults and the parents of adolescents provided written consent, whereas adolescents themselves gave verbal consent. Adolescents and adults did not differ in their age-normed scores on the Vocabulary subtest of the Wechsler Abbreviated Scale of Intelligence, Second Edition (Wechsler, 2011; $M_{\text{adolescents}} = 67.2 \pm 4.8$, $M_{\text{adults}} = 65.0 \pm 7.7$; $t(27.5) = 1.1$, $p = .29$).

Design and Materials

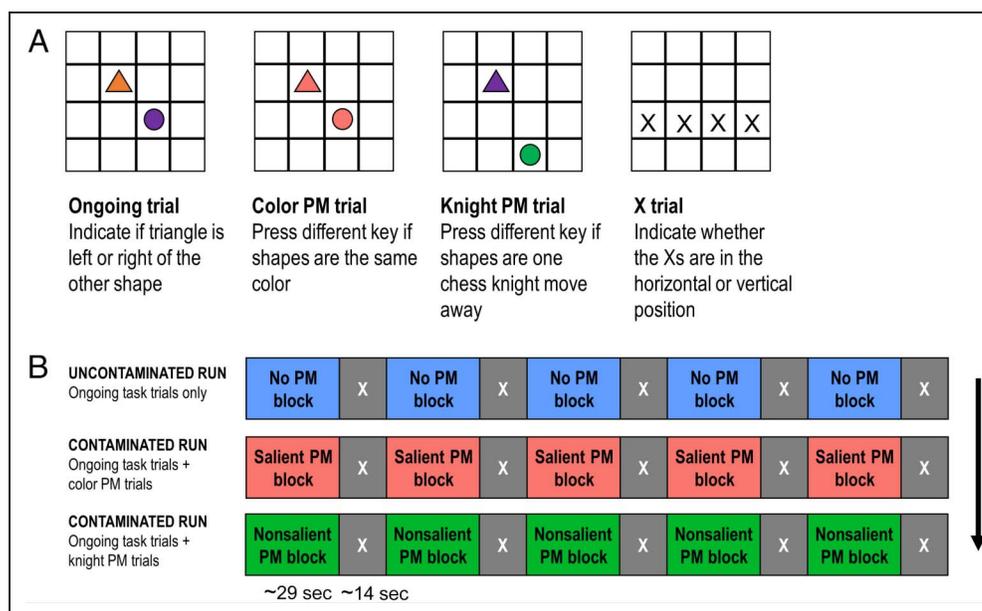
Shapes PM Task

We adapted the “shapes” experimental task from Simons et al. (2006). All PM trials were given the same intention retrieval demands, whereas the cues remained either salient or nonsalient. On each trial, two colored shapes, a triangle and another shape, appeared in various positions in

a 4×4 grid (Figure 1A). Each shape had one of six possible colors. In the OT, participants had to indicate whether the triangle shape was located to the left or right of the other shape. In the salient cue PM condition, if the shapes were the same color, participants had to press a third key (Color PM). In the nonsalient cue PM condition, participants had to press the third key if the shapes were one chess knight’s move away from each other (Knight PM). Responses were indicated by pressing one of three buttons on a handheld response box (right index finger = left, right middle finger = right, right thumb = PM trial). Shapes were never the same color in the Knight PM condition, nor in a knight configuration in the Color PM condition, to avoid competing cues and confusion for the participants. Each trial started with 500 msec of a fixation cross, followed by presentation of the stimulus (the two shapes in the 4×4 grid) for a maximum of 3000 msec, followed by 250 msec of a fixation cross at the intertrial interval. The tasks were self-paced to prevent instruction rehearsal (Burgess, Scott, & Frith, 2003).

An unrelated X task was used as an active baseline across all scanning runs (as in Simons et al., 2006). In this task, participants were asked to indicate as quickly as possible whether a series of Xs were shown on the 4×4 grid along a vertical or horizontal axis (Figure 1A). Responses were given using the right index and middle finger keys. Vertical and horizontal Xs stimuli alternated. Each trial presented the stimulus (the row of Xs) until a response was made or for a maximum of 2000 msec. A fixation cross was shown during the intertrial intervals, which varied randomly along a uniform distribution between 0 and 400 msec. The tasks were programmed in Cogent (www.vislab.ucl.ac.uk/cogent_graphics.php) running in MATLAB (The MathWorks, Inc.).

Figure 1. Shapes task. (A) Example stimuli. In the OT, participants had to indicate whether the triangle was left or right of the other shape using the left and right keys. On Color PM trials, both shapes were the same color (salient cue condition), and participants had to press a third key. On Knight PM trials, the shapes were a knight move away (nonsalient cue condition), and participants had to press the third key. On X trials, participants had to indicate whether the Xs were shown along the horizontal or vertical axis. (B) Experimental design. Participants performed three runs of the OT. The first run was uncontaminated. In the second and third runs, the OT was contaminated with Color and Knight PM trials. The order of these two runs was counterbalanced across participants.



Procedure

The tasks were administered in three runs (Figure 1B). All runs were preceded by instructions and a practice round. The first run consisted of “uncontaminated” OT trials without any expectation of a PM trial, as the PM conditions were not mentioned in the instructions of this first run. Two PM runs followed, with one run containing “contaminated” OT trials and Color PM trials (salient cue) and one run containing “contaminated” OT trials and Knight (non-salient cue) PM trials. The order of the PM runs was counterbalanced between participants. Each run consisted of five blocks of approximately 29 sec of the shapes task alternating with approximately 14 sec of the unrelated X task, with a 2-sec pause between blocks, which displayed an indication of the nature of the upcoming block (“triangle task,” “X task,” “color task,” or “knight task”). Given the self-paced nature of the design, participants differed in the total number of completed ongoing trials. Blocks of the two PM runs included up to two PM trials, which appeared no earlier than after 10 sec of OT, to ensure that the participant would be fully engaged in the OT and to control for the time between PM trials of successive blocks. In total, 10 PM trials were presented per run for both adolescents and adults. On average, adolescents completed 110 OT trials in the uncontaminated run, 94 OT trials in the Color run, and 84 OT trials in the Knight run. Adults completed 113 OT trials in the uncontaminated run, 97 OT trials in the Color run, and 88 OT trials in the Knight run.

Other Behavioral Measures

Participants completed the (1) Prospective and Retrospective Memory Questionnaire (PRMQ; Smith et al., 2000), (2) Future Orientation and Delayed Discounting Scale (FOS; Steinberg et al., 2009), and (3) Webex, a Web-based short self-report of executive functions (Buchanan et al., 2010). Participants also completed a computerized simple go/no-go task (Simmonds, Pekar, & Mostofsky, 2008) in which a “go” stimulus (green square) is presented in high frequency and requires a rapid, dominant response, which needs to be inhibited when a less frequent “no-go” stimulus (red square) is shown (Humphrey & Dumontheil, 2016). Finally, participants were administered the forward and backward digit span task in which they were required to listen to a sequence of numbers and repeat them in the same or reversed order.¹

Image Acquisition

Functional data were acquired using the Center for Magnetic Resonance Research multiband EPI sequence (Xu et al., 2013) 2× acceleration, leak block on (Cauley, Polimeni, Bhat, Wald, & Setsompop, 2014) with BOLD contrast (44 axial slices with a voxel resolution of 3 × 3 × 3 mm covering most of the cerebrum; repetition time = 2 sec, echo time =

45 msec, acquisition time = 2 sec) in a 1.5-T MRI scanner with a 30-channel head coil (Siemens TIM Avanto). Functional images were acquired in three scanning runs lasting approximately 4 min each in which around 125 volumes were obtained (time and number of volumes varied per participant given the self-paced nature of the task). The first four volumes of each run were discarded to allow for T1 equilibrium effects. A T1-weighted magnetization prepared rapid gradient echo with 2× GeneRALized Autocalibrating Partially Parallel Acquisition acceleration anatomical image lasting 5 min 30 sec was acquired before the acquisition of the three shapes task functional runs for each participant.

Data Analysis

Behavioral Data

Mean RT and accuracy analyses. Mean accuracy and RT data were analyzed using mixed repeated-measures ANOVA (rmANOVA). In all RT analyses, we only used correct ongoing trials within 2.5 SDs of each participant’s mean and excluded two trials after PM trial presentation, because participants might have still been engaged in PM processes (Ball & Brewer, 2018). First, the OT trials of the three runs were compared, using Run (Uncontaminated, Color, Knight) × Age Group (Adolescents, Adults) mixed rmANOVAs, to assess age group differences in OT performance. Second, OT and PM trials of the PM runs were analyzed with two within-participant factors (Run: Color, Knight; Condition: OT, PM) and Age group (Adolescents, Adults) as a between-participant factor. This allowed us to assess whether age groups differed in PM trial performance, accounting for differences in OT performance. Models were fitted in R (R Development Core Team, 2020) using the *afex* package (Singmann, Bolker, Westfall, Aust, & Ben-Sachar, 2020). Where necessary, Greenhouse–Geisser correction was employed for violation of sphericity and Tukey correction for multiple comparisons.

Distributional RT analyses. In addition to typical analyses of RT means, modeling RT distribution has been proposed as a useful technique to better characterize underlying profiles of cognitive control dynamics related to different processes (for details, see Ball & Brewer, 2018; Ball, Brewer, Loft, & Bowden, 2015). In PM, ex-Gaussian parameters can help investigate processes underlying monitoring and better reflect whether slower RTs are observed across task conditions (e.g., continuous monitoring, associated with the μ parameter) or whether a particular task condition has a greater relative frequency of slower RTs (e.g., transient monitoring, associated with the τ parameter). We applied the ex-Gaussian model to the OT trials RT data, using Quantile Maximum Probability Estimation software (Heathcote, Brown, & Cousineau, 2004), to obtain parameter estimates (μ , τ , σ) for each participant, separately for Uncontaminated, Color, and Knight runs, using the maximum possible number of

quantiles ($N - 1$). Acceptable model fits were obtained within 30 iterations for all participants. Parameter estimates were then analyzed using Run (Uncontaminated, Color, Knight) \times Age Group (Adolescents, Adults) mixed rmANOVAs. Visualization of the differential impact of ex-Gaussian parameters on RT can be achieved with vincentile plots of the raw RT distribution (Balota & Yap, 2011; Andrews & Heathcote, 2001). These plots were obtained separately for each run (Uncontaminated, Color, and Knight) by rank ordering raw RTs from shortest to longest for each individual and calculating the mean of the first 20%, the second 20%, and so forth.

Individual differences analyses. Exploratory Spearman correlations partialing out age were ran across age groups to assess whether measures of performance on the PM task (PM accuracy, PM RT, OT μ , OT τ , and OT σ) were associated with experimental executive function measures and questionnaire measures of PM failures and future orientation using the *psych* package (Revelle, 2019). In addition, to assess whether age-related differences in PM may be related to developmental differences in executive functioning or future orientation, original rmANOVAs were repeated with the inclusion, separately, of the forward digit score, backward digit score, no-go accuracy, or future orientation score as a mean-centered covariate.

MRI Data

MRI data preprocessing. MRI data were preprocessed and analyzed using SPM12 (Wellcome Trust Centre for Neuroimaging, www.fil.ion.ucl.ac.uk/spm/). Images were realigned to the first analyzed volume with a second-degree B-spline interpolation to correct for movement during the run. The bias-field corrected structural image was coregistered to the mean, realigned functional image and segmented based on International Consortium for Brain Mapping tissue probability maps using Montreal Neurological Institute coordinates. Resulting spatial normalization parameters were applied to the realigned images to obtain normalized functional images with a voxel size of $3 \times 3 \times 3$ mm, which were smoothed with an 8-mm FWHM Gaussian kernel.

Realignment estimates were used to calculate frame-wise displacement (FD) for each volume, which is a composite, scalar measure of head motion across the six realignment estimates (Siegel et al., 2014). Volumes with an FD > 0.9 mm were censored and excluded from general linear model (GLM) estimation by including a regressor of no interest for each censored volume. No run met criteria for exclusion, which were more than 10% of volumes censored or a root mean square (RMS) movement over the whole run greater than 1.5 mm. Adolescent and adult participants did not differ significantly in mean RMS rotational movement (adolescents = 0.17 ± 0.01 (SE), adults = 0.18 ± 0.01 ; $p = .605$). There were, however, age group differences in the mean number of censored

scans ($M_{\text{adolescents}} = 0.61 \pm 0.16$, $M_{\text{adults}} = 0.14 \pm 0.08$; $p = .013$), mean FD ($M_{\text{adolescents}} = 0.11$ mm ± 0.01 , $M_{\text{adults}} = 0.09$ mm ± 0.01 ; $p = .023$), and mean RMS translational movement ($M_{\text{adolescents}} = 0.17$ mm ± 0.02 , $M_{\text{adults}} = 0.24$ mm ± 0.03 ; $p = .042$), with more censored scans and greater mean FD but lower RMS of translations in adolescents than adults.

fMRI GLM

The volumes acquired during the three sessions were treated as separate time series. For each series, the variance in the BOLD signal was decomposed with a set of regressors in a GLM that examined sustained (block-related) and transient (event-related) activity during task performance. Three boxcar regressors represented sustained OT activity during the five blocks of each run: Uncontaminated OT, OT in Color PM run (“Color OT”), and OT in Knight PM run (“Knight OT”). Two event-related regressors represented transient PM activity in correct trials only: Color PM and Knight PM. Two additional event-related regressors represented transient activity in 10 randomly selected OT trials in each session (two per block, occurring before the PM trials), to serve as a comparison for the PM trials. Other regressors included for each run in the GLM were an event-related regressor representing the start instructions of each block and another representing the end of each block (Dumontheil, Thompson, & Duncan, 2011); a boxcar regressor representing blocks of the X task, which served as the baseline for comparison across runs; regressors representing censored volumes as covariates of no interest; and the mean over scans. Both block- and event-related regressors were convolved with the canonical hemodynamic response function. The data and model were high-pass filtered to a cutoff of 1/128 Hz.

Second-level whole-brain analyses were performed to assess sustained and transient PM-related brain activation. A first set of analyses investigated the sustained effects of maintaining intentions and compared the [OT block – Xtask block] contrasts from each of the three runs: Uncontaminated, Color, and Knight. A second set of analyses investigated transient effects in PM trials and analyzed the Color PM trials’ and Knight PM trials’ event-related first-level contrasts using the randomly selected OT trials as baseline: [Color PM trials – OT trials] and [Knight PM trials – OT trials]. These contrasts were then entered into two flexible, factorial, random effects analyses using two factors of interest with the design Participant \times Age Group (Adolescent, Adult) \times Run Type (Uncontaminated OT, Color OT, Knight OT) or Trial Type (Color PM, Knight PM), modeling Participant as a main effect (to account for the repeated-measure nature of the data) and the Age Group \times Block Type or Age Group \times Trial Type interaction.

Sustained activation in Color and Knight OT blocks compared to Uncontaminated OT blocks, transient activation in Color and Knight PM trials, and differences

between Color and Knight tasks and the interactions with Age Group were determined using the t statistic on a voxel-by-voxel basis. Statistical contrasts were used to create SPM maps thresholded at $p < .001$ uncorrected at the voxel level and whole-brain cluster familywise error (FWE) correction at $p < .05$ (corresponding to a minimum cluster size of 60 voxels for event-related analyses and 91 voxels for block-related analyses). Voxels surviving whole-brain FWE correction at $p < .05$ at the voxel level are also reported. All coordinates are given in Montreal Neurological Institute space. Region labeling was done using automatic anatomical labeling (Tzourio-Mazoyer et al., 2002). BA labeling of peak of activations was done using MRICron (Rorden & Brett, 2000). Statistical maps for all whole-brain, voxel-wise analyses are available at neurovault.org/collections/6073/.

Whole-brain correlations were run using two-sample t tests with a single covariate in SPM. In a first series of analyses, the contrast images were the average of [Color OT block – X task block in Color run] and [Knight OT block – X task block in Knight run], representing sustained activation associated with PM in the contaminated run, and the covariates were mean accuracy and RT in PM trials, FOS and PRMQ (PM), and μ . In a second series of analyses, the contrast images were the average of [Color PM trials – OT trials] and [Knight PM trials – OT trials], representing transient activation associated with PM, and the covariate was τ .

Exploratory analyses. As other studies suggest improvement in performance until 13–14 years old (Bowman et al., 2015; Altgassen et al., 2014; Wang et al., 2006, 2011; Zöllig et al., 2007), two series of exploratory analyses were carried out. First, the adolescent sample was split into 14 younger adolescents from 12 to 14 years old ($M = 13.1$, $SD = 0.7$) and 14 older adolescents from 15 to 17 years old ($M = 15.5$, $SD = 0.5$), and their behavioral and fMRI data were compared with those of adults. Second, associations with age as a continuous measure were assessed within the adolescent sample.

RESULTS

Behavioral Results

Accuracy and RT Analyses of Trial Type and Cue Salience

First analyses compared the OT trials of the three runs (Uncontaminated, Color, Knight) in Run \times Age Group mixed rmANOVAs (Table 1). Adolescents ($M = 93.7\%$ [$SE = 0.8$]) were less accurate than adults ($M = 96.7\%$ [0.8]; Figure 2A), but accuracy was not affected by the PM tasks. In contrast, RTs were slower in OT trials in the Knight run ($M = 762$ msec [16]) than the Color run ($M = 650$ msec [16]), $t(36) = 5.8$, $p < .0001$, and fastest in the Uncontaminated run ($M = 584$ msec [16]), $t(36) = 9.9$, $p < .0001$ (Figure 2B). There was no

main effect of Run on accuracy, main effect of Age group on RT, or Run \times Age Group interaction on either accuracy or RT. Exploratory analyses indicated that the difference in accuracy between age groups was driven by trend-level poorer performance in younger ($M = 94.6\%$ [1.0]), $t(44) = 2.2$, $p = .08$, and older ($M = 93.9\%$ [1.1]), $t(44) = 2.4$, $p = .05$, adolescents than adults ($M = 97.5\%$ [1.0]). There was no significant effect of or interaction with age (as a continuous predictor) within the adolescent sample for either accuracy or RT (all F s < 0.2 and p s $> .15$).

The second set of analyses compared PM and OT trials in the two PM runs in Run (Color, Knight) \times Trial Type (PM, OT) \times Age Group mixed rmANOVAs. Participants were more accurate on OT trials ($M = 95.5\%$ [1.2]) than PM trials ($M = 76.5\%$ [1.2]), and adolescents ($M = 83.2\%$ [1.3]) were again overall less accurate than adults ($M = 88.5\%$ [1.3]; Table 1), but there was no main effect of Run or significant two- or three-way interactions (Figure 2A). Exploratory analyses comparing younger and older adolescents to the adult group demonstrated that the main effect of Age group was driven by younger adolescents ($M = 81.8\%$ [1.5]), who were less accurate than adults ($M = 89.0\%$ [1.4]), $t(44) = 3.7$, $p = .0017$, while older adolescents had intermediary accuracy ($M = 86.6\%$ [1.6]) and did not differ from younger adolescents or adults (p s $\geq .10$). In addition, there was a significant Trial Type \times Age Group interaction indicating that younger adolescents were less accurate in PM trials than older adolescents ($\Delta M = 9.9\%$ [3.0]), $t(87) = 3.3$, $p = .003$, and adults ($\Delta M = 11.2\%$ [2.6]), $t(87) = 4.2$, $p = .0001$, but did not differ from older adolescents on OT trials (p s $> .43$). Older adolescents and adults did not differ on either PM or OT trials (p s $> .41$). Consistent with these age group analyses, exploratory analyses within the adolescent group showed a significant linear increase in accuracy with Age, $F(1, 26) = 5.09$, $p = .03$, $\eta_p^2 = .05$; however, the Trial Type \times Age interaction was not significant, $F(1, 26) = 0.02$, $p = .89$.

For RT data (Table 1), participants were faster on OT trials ($M = 709$ msec [18]) than PM trials ($M = 834$ msec [18]) and faster in the Color run ($M_{\text{Color}} = 703$ msec [19]) than the Knight run ($M = 839$ msec [19]). In addition, the interaction between Trial type and Run was significant: The difference between Knight and Color runs was greater for PM trials ($\Delta M = 159$ msec [19]) than for OT trials ($\Delta M = 111$ msec [18]; Figure 2B). Adolescents ($M = 809$ msec [25]) were slower than adults ($M = 733$ msec [25]), but a significant Trial Type \times Age Group interaction indicated that the age group difference was driven by PM trials ($\Delta M = 97$ msec [37]), $t(51.1) = 2.6$, $p = .01$, with no difference in OT trials ($\Delta M = 53$ msec [37]), $t(51.1) = 1.5$, $p = .15$ (Figure 2B). Neither the interaction between Run and Age group nor the three-way interaction was significant. Exploratory analyses with the split adolescent groups showed similar results. Whereas the main effect of Age group did not reach significance (Table 1), the interaction between Trial type and Age group showed that younger adolescents

Table 1. Statistical Results of the Behavioral Age Group Analyses

Measure	Effects	Age Group: Adolescents, Adults	Age Group: Younger Adolescents, Older Adolescents, Adults
<i>OT trials: Run (Uncontaminated, Color, Knight) × Age Group</i>			
Accuracy	Age group	$F(1, 45) = 7.3, p = .01, \eta_G^2 = .11^a$	$F(2, 44) = 3.7, p = .03, \eta_G^2 = .12^a$
	Run	$[F(1.5, 67.4) = 1.6, p = .33]$	$[F(1.5, 66.1) = 0.8, p = .43]$
	Age Group × Run	$[F(1.5, 67.4) = 0.5, p = .55]$	$[F(3, 66.1) = 0.4, p = .76]$
RT	Age group	$[F(1, 45) = 2.6, p = .11]$	$[F(2, 44) = 1.5, p = .25]$
	Run	$F(1.2, 51.6) = 96.1, p < .001, \eta_G^2 = .31$	$F(1.2, 50.4) = 102.2, p < .001, \eta_G^2 = .33$
	Age Group × Run	$[F(1.5, 51.6) = 1.3, p = .26]$	$[F(2.3, 50.4) = 0.9, p = .44]$
<i>Run (Color, Knight) × Trial Type (OT, PM) × Age Group</i>			
Accuracy	Age group	$F(1, 45) = 8.9, p = .005, \eta_G^2 = .06^a$	$F(2, 44) = 6.9, p < .002, \eta_G^2 = .09^a$
	Trial type	$F(1, 45) = 135.4, p < .001, \eta_G^2 = .43$	$F(1, 44) = 148.5, p < .001, \eta_G^2 = .44$
	Age Group × Trial Type	$[F(1, 45) = 1.4, p = .25]$	$F(2, 44) = 4.2, p = .02, \eta_G^2 = .04$
	Run	$[F(1, 45) = 2.9, p = .10]$	$[F(1, 44) = 2.9, p = .09]$
	Age Group × Run	$[F(1, 45) < 0.1, p = .86]$	$[F(2, 44) < 0.1, p = .98]$
	Trial Type × Run	$[F(1, 45) = 2.0, p = .25]$	$[F(1, 44) = 2.0, p = .17]$
	Age Group × Run × Trial Type	$[F(1, 45) < 0.1, p = .97]$	$[F(2, 44) < 0.1, p = .99]$
RT	Age group	$F(1, 45) = 4.5, p = .04, \eta_G^2 = .07^b$	$[F(1, 44) = 2.6, p = .09]$
	Trial type	$F(1, 45) = 183.1, p < .001, \eta_G^2 = .17$	$F(1, 44) = 200.1, p < .0001, \eta_G^2 = .18$
	Age Group × Trial Type	$F(1, 45) = 5.5, p = .02, \eta_G^2 = .006^a$	$F(2, 44) = 4.2, p = .02, \eta_G^2 = .009^a$
	Run	$F(1, 45) = 59.9, p < .001, \eta_G^2 = .19$	$F(1, 44) = 61.9, p < .001, \eta_G^2 = .21$
	Age Group × Run	$[F(1, 45) = 0.7, p = .41]$	$[F(2, 44) = 0.3, p = .71]$
	Trial Type × Run	$F(1, 45) = 12.8, p < .001, \eta_G^2 = .008$	$F(1, 44) = 9.9, p = .003, \eta_G^2 = .006$
	Age Group × Run × Trial Type	$[F(1, 45) = 0.2, p = .64]$	$[F(2, 44) = 1.3, p = .30]$

Nonsignificant effects are put in square brackets.

^aEffect remained significant when forward digit score, backward digit score, no-go accuracy, or future orientation score was included as a centered covariate.

^bEffect became nonsignificant when forward digit score, backward digit score, no-go accuracy, or future orientation score was included as a centered covariate.

were significantly slower than adults on PM trials ($\Delta M = 120$ msec [41]), $t(49.7) = 2.9, p = .02$, but not on OT trials ($\Delta M = 61$ msec [41]), $t(49.7) = 1.5, p = .31$. Older adolescents did not differ from either age group on either type of trials (all $ps > .38$). Exploratory analyses within the adolescent group revealed no main effect of age (as a continuous predictor) or interactions with age (all $Fs < 3.1$ and $ps > .09$).

Ex-Gaussian Analyses

Ex-Gaussian analyses focused on the OT RT data (Table 2). Run (Uncontaminated, Color, Knight) × Age Group (Adolescents, Adults) mixed rmANOVAs, revealed a main effect of Run for all three estimates (Table 2),

but with different patterns. μ estimates were higher in the Knight run than the Color run, $t(90) = 7.2, p = .007$, and higher in both the Knight, $t(90) = 10.3, p < .0001$, and Color, $t(90) = 3.1, p < .0001$, runs than in the Uncontaminated run. There was therefore a modal shift of the overall RT distribution (μ) in ongoing trials of the PM runs that was greater in the Knight task than in the Color task (Figure 3). τ was higher in the Knight run than in the Uncontaminated run, $t(90) = 2.6, p = .025$, and there was a trend for higher τ for the Color run than the Uncontaminated run, $t(90) = 2.3, p = .054$, but no difference between Knight and Color runs, $t(90) = 0.31, p = .94$. Color and Knight tasks were therefore associated with a similar increased frequency of slow RTs (Figure 3). σ Estimates were higher in the Knight run

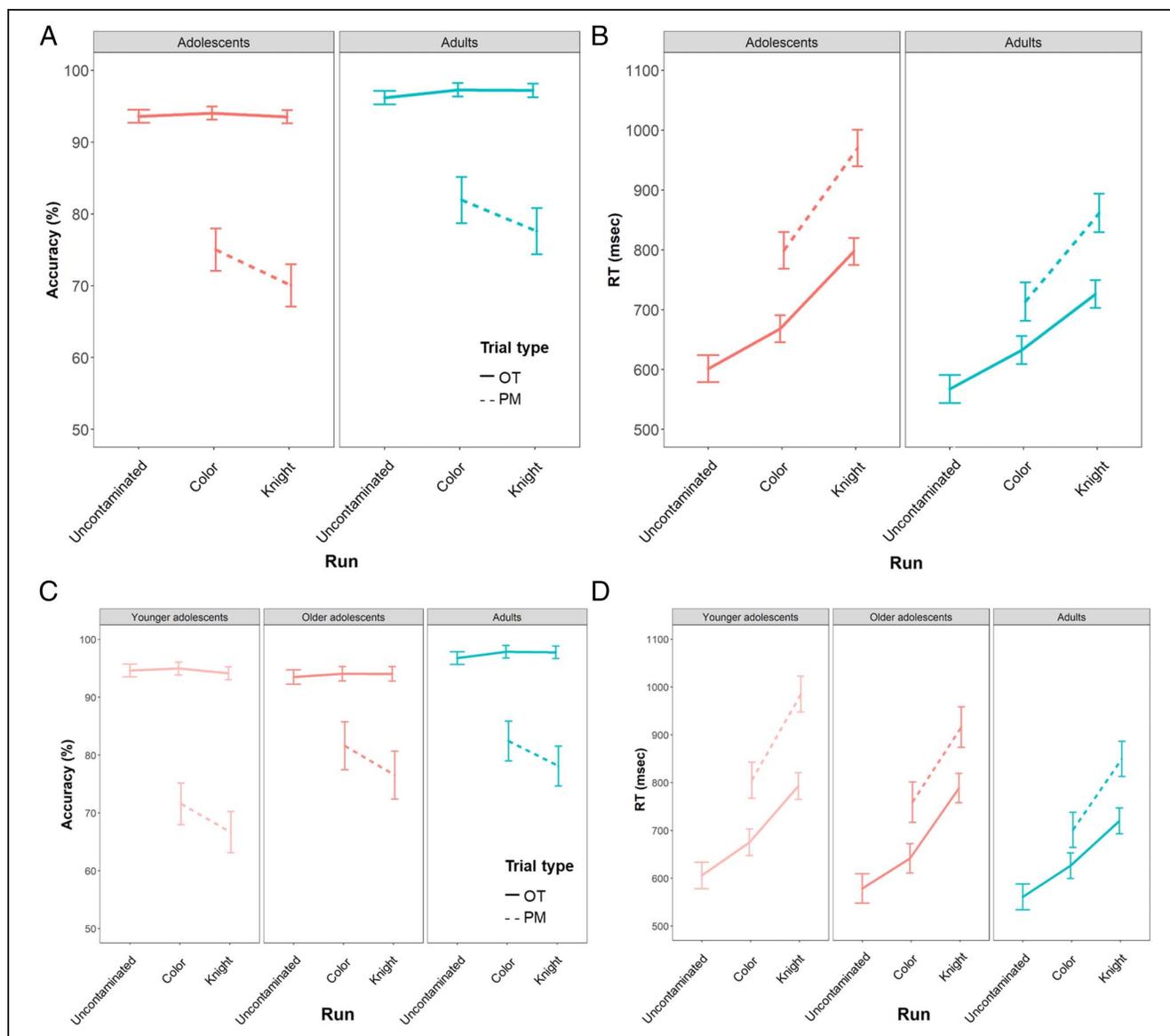


Figure 2. Mean accuracy (A, C) and RT (B, D) as a function of Run, Trial type, and Age group. Top row shows the results with the original groups of adolescents ($n = 28$) and adults ($n = 19$). Bottom row shows the results when the adolescent group is divided into younger adolescents ($n = 14$, 12–14 years old) and older adolescents ($n = 14$, 15–17 years old). Error bars represent *SE*. OT = OT trials; PM = PM task trials.

than in the Uncontaminated, $t(90) = 7.3$, $p < .0001$, and Color, $t(90) = 6.9$, $p < .0001$, runs, with no difference between Color and Uncontaminated runs, $t(90) = 0.3$, $p = .93$, suggesting increased overall variability in the

Knight OT. There were no significant main effects of Age group or Run \times Age Group interaction ($ps > .08$), except for the τ estimate. A main effect of Age group, $F(1,45) = 7.7$, $p = .008$, $\eta_G^2 = .08$, indicated that

Table 2. Results of the Ex-Gaussian Analyses of the Ongoing Trials' RT Data

	Uncontaminated Run, Mean (SE)	Color Run, Mean (SE)	Knight Run, Mean (SE)	Main Effect of Run
RT (msec)	584 (16)	650 (16)	762 (16)	$F(1.2, 51.6) = 96.2$, $p < .001$, $\eta_G^2 = .31$
μ (msec)	497 (15)	544 (15)	653 (15)	$F(1.2, 53.7) = 55.9$, $p < .001$, $\eta_G^2 = .29$
τ (msec)	87 (7)	106 (7)	109 (7)	$F(1.4, 60.9) = 4.2$, $p < .03$, $\eta_G^2 = .04$
σ (msec)	51 (5)	52 (5)	96 (5)	$F(1.3, 58.2) = 33.6$, $p < .001$, $\eta_G^2 = .27$

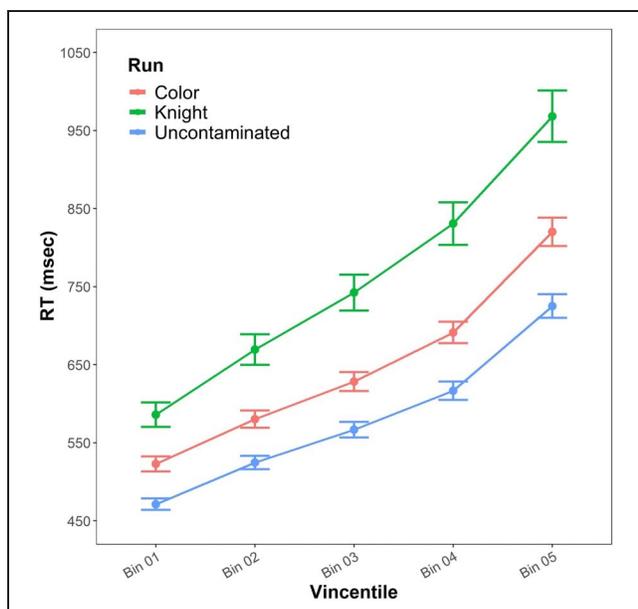


Figure 3. Vincentile plot for OT trials of the Uncontaminated and Contaminated runs. Vincentile plots depict the data without prior assumptions of its distribution by plotting mean rank-ordered RTs of equipopulated bins as a function of Run (Balota & Yap, 2011; Andrews & Heathcote, 2001). The plot illustrates the effects of maintaining an intention: Both the Color and Knight runs show an overall slowing of RTs (associated with the μ parameter) as well as a stretch of the upper tail (slower RTs) of the distribution (which corresponds to the τ parameter). Error bars indicate *SE*.

adolescents had more frequent slow RTs (higher τ estimates, $M = 115$ msec [$SE = 7$]) than adults ($M = 87$ msec [7]). Exploratory analyses with the split adolescent groups indicated age group differences were driven by the younger adolescents. There was a main effect of Age group, $F(2, 44) = 7.1$, $p = .002$, $\eta_p^2 = .14$: Younger adolescents had overall higher τ estimates ($M = 125$ msec [8]) than older adolescents ($M = 96$ msec [8]), $t(90) = 3.7$, $p = .001$, and adults ($M = 82.2$ [7.9]), $t(90) = 2.3$, $p = .05$, whereas older adolescents and adults did not differ, $t(44) = 1.2$, $p = .47$. Exploratory analyses within the adolescent group revealed no significant main effect of age or interaction between Run and Age (all F s < 4.1 and p s $\geq .05$), although, consistent with the three age group analyses, the effect of age on τ was at the trend level, $F(1, 26) = 4.1$, $p = .05$.

Other Behavioral Measures of Executive Function, PM Failures, and Future Orientation

Adults had higher backward digit span scores than adolescents, and there was a trend for greater future orientation in adults than adolescents. The other measures did not show age group differences (Table 3). Spearman correlation analyses partialing out age showed that PM accuracy was negatively associated with WebExec ($r = -.34$, $p = .02$) and PRMQ (PM; $r = -.32$, $p = .03$) scores, which are indices of executive functioning and PM failures in daily life, respectively. Correlations between PM RT, OT

Table 3. Behavioral Measures of Executive Functions, PM, and Future Orientation

	Adolescents, Mean (SE)	Adults, Mean (SE)	Age Group Comparison
<i>PM^a</i>			
PRMQ (PM subscale; 8–40)	22.0 (0.7)	20.6 (0.8)	$t(45) = 1.4$, $p = .17$
PRMQ (RM subscale; 8–40)	19.1 (0.9)	19.4 (0.9)	$t(45) = 0.3$, $p = .76$
<i>Future orientation</i>			
FOS (1–4) ^b	2.9 (0.1)	3.1 (0.1)	$t(43) = 1.9$, ^c $p = .06$
<i>Executive functions</i>			
WebExec (6–24) ^d	13.5 (0.5)	12.8 (0.7)	$t(45) = 0.9$, $p = .42$
Forward digit span score (1–22)	16.8 (0.7)	18.2 (0.8)	$t(45) = 1.4$, $p = .18$
Backward digit span score (1–22) ^e	9.0 (0.6)	12.2 (0.8)	$t(44) = 3.5$, $p = .001$
No-go accuracy (%)	87.7 (1.7)	91.2 (2.1)	$t(45) = 1.4$, $p = .16$

Summary statistics of measures collected in adolescent and adult participants. The possible range for each measure is given in brackets. FOS = Future Orientation and Delayed Discounting Scale; PRMQ = Prospective and Retrospective Memory Questionnaire; RM = retrospective memory.

^aHigher scores indicate more PM and RM failures.

^bHigher scores indicate stronger future orientation.

^cOne adult and one adolescent participant did not complete the FOS.

^dHigher scores indicate more executive functioning failures.

^eOne adolescent participant did not complete the backward digit span task.

Table 4. Sustained Neuroimaging Results across Age Groups

<i>Region</i>	<i>L/R</i>	<i>Extent</i>	<i>t Value</i>	<i>x</i>	<i>y</i>	<i>z</i>	<i>BA</i>
<i>Color OT > Uncontaminated OT</i>							
Insula	R	1111 ^a	8.21 ^b	33	26	2	47
Inferior frontal gyrus (operculum)	R		7.16 ^b	42	8	29	44
Middle frontal gyrus	R		5.82 ^b	39	2	53	6
Pre-SMA	R	218 ^a	6.09 ^b	6	20	50	8
Inferior parietal lobule	L	505 ^a	5.90 ^b	-45	-37	50	40
Superior parietal lobule	L		5.32 ^b	-27	-64	56	7
Inferior parietal lobule	R	546 ^a	5.64 ^b	33	-55	53	7
Supramarginal gyrus	R		5.26 ^b	45	-34	44	40
Insula	L	147 ^a	5.45 ^b	-30	26	-1	47
Cerebellum	L	186 ^a	4.99 ^b	-6	-79	-19	
Cerebellum	L		4.87 ^b	-27	-73	-22	
<i>Knight OT > Uncontaminated OT</i>							
Inferior parietal lobule	L	1515 ^a	10.56 ^b	-45	-37	47	40/2
Superior parietal lobule	L		9.92 ^b	-15	-67	56	7
Middle occipital gyrus	L		6.81 ^b	-27	-70	29	19
Supramarginal gyrus	R	1944 ^a	9.90 ^b	39	-37	44	40
Superior parietal lobule	R		9.26 ^b	27	-64	53	7
Middle occipital gyrus	R		5.87 ^b	33	-79	14	19
Insula	R	1703 ^a	9.79 ^b	33	26	2	47
Precentral gyrus	R		9.19 ^b	45	8	29	44
Middle frontal gyrus	R		6.54 ^b	33	2	59	6
Inferior frontal gyrus	L	162 ^a	7.38 ^b	-30	20	-1	47
Pre-SMA	R	295 ^a	7.21 ^b	6	20	50	8
Inferior frontal gyrus (operculum)	L	189 ^a	6.88 ^b	-42	5	26	44
Inferior temporal gyrus	R	751 ^a	6.75 ^b	48	-52	-7	37
Fusiform	L		6.42 ^b	-30	-73	-19	19
Cerebellum	L		5.91 ^b	-9	-79	-19	
Superior frontal gyrus	L	244 ^a	6.29 ^b	-24	2	62	6
<i>Color OT > Knight OT</i>							
Midcingulate cortex	L	365 ^a	4.83 ^b	-12	-49	35	23
Midcingulate cortex			3.97	0	-22	41	23
Midcingulate cortex	R		3.93	12	-46	35	23
Angular gyrus	R	191 ^a	4.83 ^b	57	-58	35	39
Angular gyrus	R		4.07	45	-67	50	39
Superior frontal gyrus	L	108 ^a	4.68	-15	41	47	1
Angular gyrus	L	159 ^a	4.62	-45	-70	44	39

Table 4. (continued)

Region	L/R	Extent	<i>t</i> Value	<i>x</i>	<i>y</i>	<i>z</i>	BA
Supramarginal gyrus	L		3.71	-60	-55	32	40
<i>Knight OT > Color OT</i>							
Precuneus	L	2067 ^a	7.37 ^b	-15	-67	56	7
Superior parietal lobule	R		6.79 ^b	18	-61	56	7
Supramarginal gyrus	R		6.60 ^b	36	-40	44	40
Superior frontal gyrus	R	95 ^a	4.63	24	8	56	6/8

Coordinates and *t* values are listed for regions showing a significant difference in sustained BOLD signal for [Color OT block > Uncontaminated OT block], [Knight OT block > Uncontaminated OT block], and the comparison between the two. Blocks of the X task were used as a baseline common across runs. L/R = left/right hemisphere; OT = ongoing task; pre-SMA = pre-supplementary motor area.

^aCluster significant at $p_{FWE} < .05$, with a cluster-defining threshold of $p < .001$ uncorrected at the voxel level.

^bVoxel significant at $p_{FWE} < .05$.

μ , OT τ , and OT σ and questionnaire measures of executive functioning and PM and future orientation were not significant (all $ps > .21$).

To assess whether observed developmental differences in PM task measures may have been related to developmental differences in executive functioning or future orientation, the rMANOVAs ran above that showed significant main effects or interactions with Age Group (Adolescents, Adults) were repeated with the inclusion, separately, of the forward digit score, backward digit

score, no-go accuracy, or future orientation score as a centered covariate. Results showed that the significant main effects of Age on accuracy and interactions of Age Group with Run and Trial Type on RT remained significant when these covariates were included. However, the main effect of Age Group on RT in contaminated runs, which indicated slower RTs in adolescents than adults across OT and PM trials, became nonsignificant when forward digit score, backward digit score, no-go accuracy, or future orientation was entered as a covariate (Table 1).

Figure 4. Sustained fMRI results across age groups. Regions showing differences in BOLD between ongoing task (OT) blocks between the Uncontaminated, Color, and Knight runs are rendered on the SPM12 mesh template. Blocks of the X task were used as baseline common across runs. From left to right: lateral view of the left hemisphere and medial and lateral views of the right hemisphere. Threshold: cluster significant at $p_{FWE} < .05$, with a cluster-defining threshold of $p < .001$ uncorrected at the voxel level.

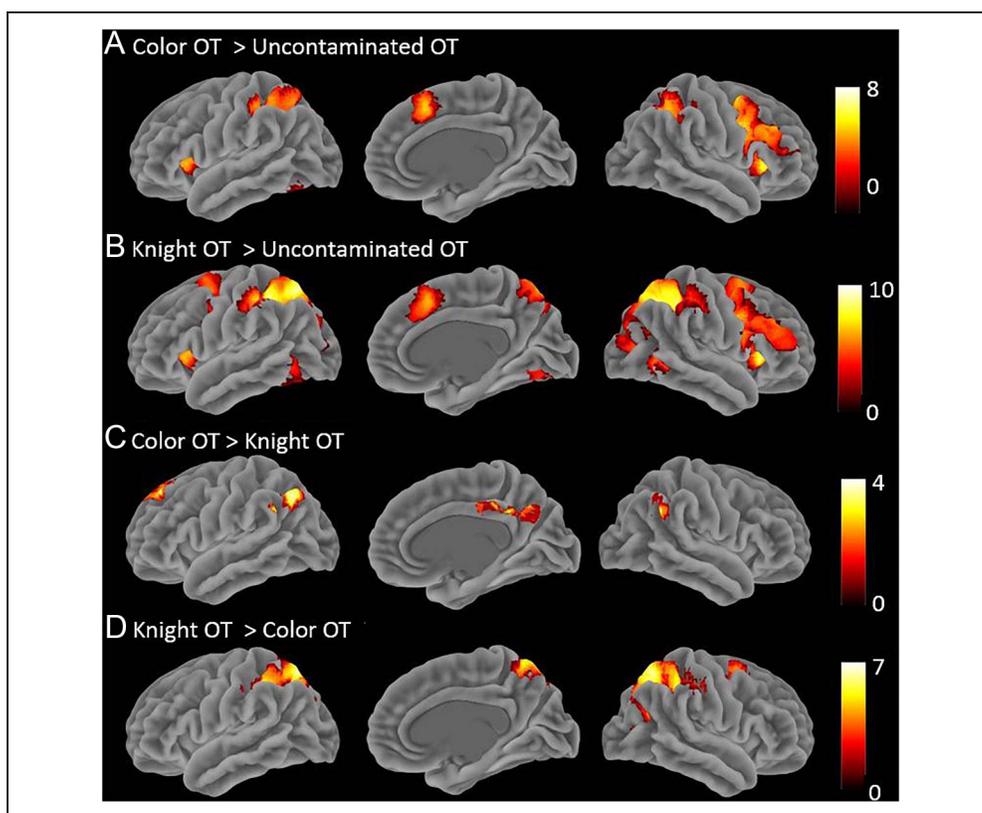


Table 5. Transient Neuroimaging Results across Age Groups

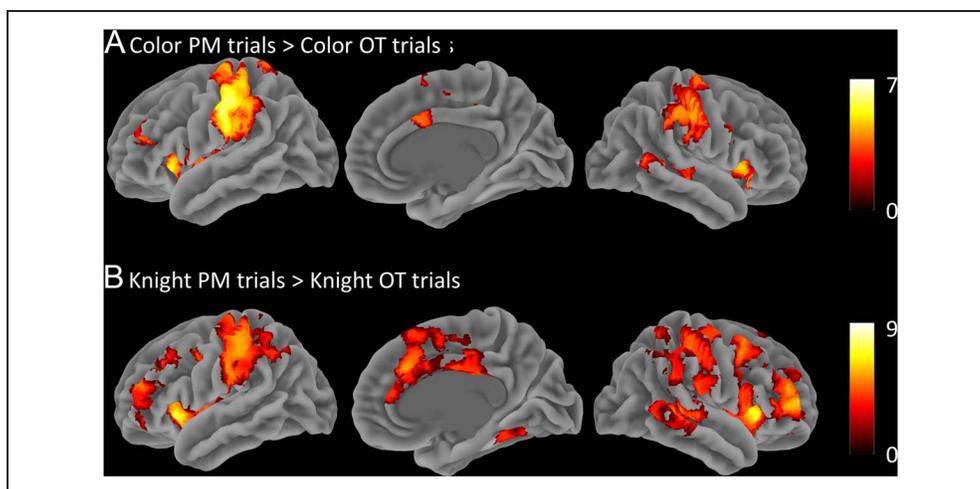
Region	L/R	Extent	<i>t</i> Score	<i>x</i>	<i>y</i>	<i>z</i>	BA
<i>Color PM trials > Color OT trials</i>							
Postcentral gyrus	L	1489 ^a	7.45 ^b	-60	-22	41	3
Precentral gyrus	L		6.61 ^b	-33	-22	71	6
Postcentral gyrus	L		6.13 ^b	-48	-31	59	3/2
Insula	R	158 ^a	5.76 ^b	36	17	-1	48
Postcentral gyrus	R	574 ^a	5.60 ^b	57	-22	53	3
Postcentral gyrus	R		4.48	60	-16	32	43
Postcentral gyrus	R		4.43	42	-40	62	2
Mid cingulate cortex	L	274 ^a	4.98	-9	5	38	24
SMA	R		3.99	3	11	62	6
Superior frontal gyrus	R	94 ^a	4.95	33	-7	65	6
Mid temporal gyrus	R	166 ^a	4.84	48	-25	-7	21
Mid temporal gyrus	R		4.47	57	-43	2	22
Precentral gyrus	R	80 ^a	4.76	57	11	32	6/44
Middle frontal gyrus	L	99 ^a	4.46	-36	41	29	46
Mid cingulate cortex	L	72 ^a	4.23	-12	-28	47	23
SMA	R		3.96	9	-22	47	23
<i>Knight PM Trials > Knight OT Trials</i>							
Insula	R	3243 ^a	7.82 ^b	39	17	-1	48
Mid temporal gyrus	R		6.87 ^b	57	-40	2	22
Middle frontal gyrus	R		6.61 ^b	42	50	8	46/10
Postcentral gyrus	L	1476 ^a	6.14 ^b	-45	-28	50	3
Postcentral gyrus	L		6.01 ^b	-57	-19	35	48
Precentral gyrus	L		5.25	-33	-22	71	6
Mid cingulate cortex	R	1379 ^a	6.35 ^b	9	29	32	32
Mid cingulate cortex	L		5.52 ^b	0	-10	32	23
SMA	R		4.87	6	17	56	6
Insula	L	700 ^a	9.40 ^b	-33	20	-7	47
Insula	L		5.44 ^b	-36	-1	2	48
Middle frontal gyrus	L	444 ^a	5.59 ^b	-33	47	17	5
Middle frontal gyrus	L		5.13	-39	32	35	46
Precentral gyrus	L		4.70	-45	5	44	6
Fusiform gyrus	R	269 ^a	5.27	24	-58	-16	37
Vermis			3.83	3	-67	-28	
Caudate	R	100 ^a	5.61 ^b	12	2	17	
Thalamus	R		3.84	9	-19	8	

Coordinates and *t* values are listed for regions showing a significant difference in transient BOLD signal between Color PM, Knight PM, and OT trials. L/R = left/right hemisphere; OT = ongoing task; PM = prospective memory; SMA = supplementary motor area.

^aCluster significant at $p_{FWE} < .05$ at the cluster level, with a cluster-defining threshold of $p < .001$ uncorrected at the voxel level for the Color PM trials > Color OT trials contrast and $p < .0001$ uncorrected for the Knight PM trials > Knight OT trials contrast. This more stringent contrast was used to better differentiate the observed clusters.

^bVoxel significant at $p_{FWE} < .05$.

Figure 5. Transient fMRI results across age groups. Regions showing increased BOLD signal in prospective memory (PM) trials compared to randomly selected ongoing task (OT) trials are rendered on the SPM12 mesh template. From left to right: lateral view of the left hemisphere and lateral and medial views of the right hemisphere. Threshold: cluster significant at $p_{FWE} < .05$, with a cluster-defining threshold of $p < .001$ uncorrected at the voxel level.



Neuroimaging Results

Intention Maintenance

Sustained activation during the OT blocks was compared between runs, using blocks of the X task, common across runs, as a baseline, for all comparisons. Compared to OT blocks in the Uncontaminated run, OT blocks in the Color run were associated with higher BOLD signal in a large cluster in the right hemisphere with peak activation in the insula, extending into the right lateral middle frontal gyrus cluster and rostrally into the frontal pole. The left insula/frontal operculum also showed increased BOLD signal in this contrast, as well as the left fusiform gyrus and the left cerebellum. The other observed clusters were bilateral and located in the inferior parietal lobules and along the medial wall in the pre-SMA (Table 4, Figure 4A).

OT blocks in the Knight run exhibited similar but greater overall activation than in the Color run when compared to the Uncontaminated run. The right frontal and bilateral parietal clusters were larger, and the latter extended to the medial wall and into the middle occipital gyri. There was also an additional cluster in the left precentral gyrus (Table 4, Figure 4B).

Comparing Color OT blocks to Knight OT blocks revealed higher activation in bilateral angular gyri, left supramarginal gyrus, and a cluster in the superior medial frontal cortex, reflecting less decreases in BOLD signal compared to X-task baseline blocks in the Color run than in the Knight run (Table 4, Figure 4C). Comparing Knight OT blocks to Color OT blocks revealed higher activations of the right superior frontal gyrus and bilateral superior and inferior parietal lobules, in regions that showed overall greater activation in the contaminated than the uncontaminated runs, and greater activation in OT blocks than X task blocks (Table 5, Figure 4D).

PM Trial Execution

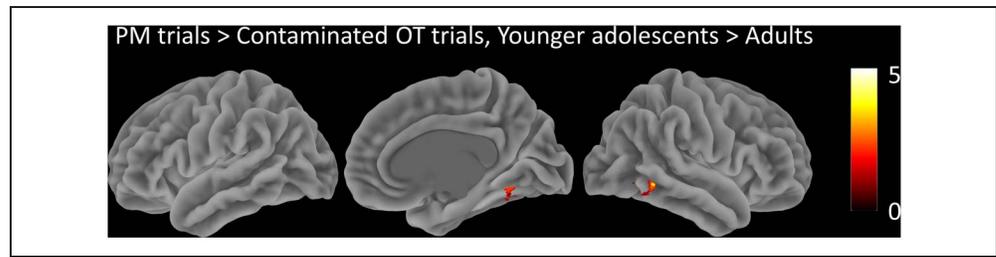
Transient effects during PM trials were investigated by contrasting event-related changes in BOLD signal during

PM trials to a randomly selected subset of OT trials performed within the same run. Color PM trials were associated with strong activation along the precentral and postcentral gyri bilaterally, extending into the supramarginal gyri; frontal activation in the left inferior and middle frontal gyri as well as bilateral anterior insula; and activation along the medial wall in clusters in the mid-cingulate cortex and pre-SMA or SMA as well as in the right middle temporal gyrus (Table 5, Figure 5). Knight PM trials were associated with a similar but broader network of brain regions, with additional clusters in the frontal cortex bilaterally and in the right parietal and temporal cortex. A more conservative threshold of $p < .0001$ uncorrected at the voxel level was used to differentiate the clusters observed in this contrast presented in Table 5 and Figure 5. There was a bilateral activity in the frontal poles (RLPFC), which extended posteriorly into inferior and middle frontal gyri including DLPFC and VLPFC. There was activation of bilateral AI. On the medial wall, there was activation that extended from ACC to the SMA and mid-cingulate cortex. In the parietal lobes, bilateral superior and inferior activation was observed, as well as precentral and postcentral gyri activation. Finally, there was activation of the right middle temporal gyrus as well as of subcortical structures: the caudate and putamen. No regions showed an impact of cue salience, that is, differences in event-related BOLD signal between Color PM and Knight PM trials, when controlling for contaminated OT trials.

Age Group Differences

Adolescents and adults did not show differences in patterns of activation in any of the sustained or transient BOLD signal change contrasts. Exploratory analyses comparing the younger, older adolescent, and adult groups showed greater activation in the young adolescent group compared to the adult group in PM trials than in contaminated OT trials in a posterior cluster (119 voxels) located

Figure 6. Comparison of transient changes in activation between younger adolescents and adults. A single cluster showed a greater increase in BOLD signal in younger adolescents than adults in prospective memory (PM) trials (averaging Color and Knight trials) compared with Uncontaminated ongoing task



(OT) trials. Results are rendered on the SPM12 mesh template. From left to right: lateral view of the left hemisphere and medial and lateral views of the right hemisphere. Threshold: cluster significant at $p_{FWE} < .05$, with a cluster-defining threshold of $p < .001$ uncorrected at the voxel level.

in the right fusiform ([36, -52, -13], BA 37, $t = 5.24$), inferior temporal gyrus ([48, -49, -7], BA 17, $t = 4.54$), and inferior occipital gyrus ([36, -67, -10], BA 19, $t = 3.99$; Figure 6). There were no other significant differences between these age groups. Additional exploratory analyses assessed whether brain activation was associated with age as a continuous measure in the adolescent sample. No significant associations were observed.

Covariate Analyses

Whole-brain analyses were performed to investigate correlations between the self-reported measure of FOS, PRMQ (PM), and μ and sustained BOLD signal during contaminated trials in OT blocks (averaging across cue salience) and τ and transient BOLD signal during PM trials. No significant association was observed.

DISCUSSION

We examined the impact of cue salience on event-based PM and whether differences exist between adolescents and adults. To characterize sustained and transient processes associated with PM, we supplemented analyses of mean indices of performance. We used ex-Gaussian modeling of RT distribution to distinguish patterns of slowing associated with PM interference. We also used a mixed block/event-related fMRI design, which allowed the investigation of sustained effects associated with maintaining PM intentions and transient effects associated with PM trial execution. We show that adults remember to execute delayed intentions better than young adolescents and provide some evidence that this ability develops across the adolescent age range in this study (12–17 years). High cue salience facilitated PM performance and influenced sustained activation during the OT. However, contrary to predictions, cue salience did not interact with age. Adolescents and adults showed similar modulation of performance and neural activity by cue salience as well as broadly similar behavioral and neural correlates of PM.

Behavioral Results

PM Intention Maintenance (OT Trials)

In comparison to the uncontaminated run, intention maintenance throughout contaminated runs was associated with slower mean RTs but similar accuracy. We manipulated one of the main retrieval-based factors, cue salience, to explore the underlying cognitive processes related to its facilitation effect on performance. The two PM conditions were designed to elicit a greater need for proactive monitoring of the Knight PM cues than the Color PM cues and, reversely, the possibility to rely to a greater extent on reactive control for the detection of the salient Color PM cues. Consistent with the task design, monitoring costs varied as a function of cue salience, with relatively slower RTs for ongoing trials of the Knight run, with nonsalient PM cues, than the Color run, with salient PM cues. There was no difference in OT accuracy between PM conditions. This suggests that nonsalient cues had higher intention maintenance and cue monitoring demands that detracted from speed, but not accuracy, performance of the OT. To the extent that perceptually salient cues can elicit an orienting response (Kliegel et al., 2013; McDaniel & Einstein, 2000), they can be more reliant on bottom-up attentional processes (Smith & Bayen, 2004; Smith, 2003), reducing the need for controlled monitoring. In contrast, low cue salience can cause shifts toward the use of proactive above reactive control mechanisms, as more strategic monitoring (vs. automatic retrieval) is needed for successful performance.

Mean RT interference costs have been well documented in PM paradigms (Smith, 2003) and can be interpreted as evidence for monitoring activities in the context of competition for limited cognitive control resources (Altgassen et al., 2017). Alternative interpretations posit that increased latencies can be related to target-checking strategies before and after the ongoing decision (Horn & Bayen, 2015) or that they could relate to lapses in attention (Ball & Brewer, 2018).

Standard RT cost analyses were followed up with ex-Gaussian distribution modeling, which has been suggested to differentiate between sustained (associated with the μ parameter) and transient (associated with the τ parameter)

PM-induced cost effects (Ball & Brewer, 2018; Loft et al., 2014; Abney et al., 2013). Intention maintenance was associated with an overall shift in the distribution (μ), which was highest for the condition with nonsalient PM cues and is reflective of the increased RTs described above. A μ cost has been proposed as an important indicator of slowing because of PM processes (Ball & Brewer, 2018), which suggests that sustained monitoring is particularly increased in ongoing trials of the Knight task, when the PM cue is less salient. However, the μ parameter was not correlated with sustained BOLD activity in the contaminated runs. A second parameter, σ , which captures variability of the normal distribution (Gmehlin et al., 2016; Vaurio, Simmonds, & Mostofsky, 2009), was increased in the Knight run compared to the Color and Uncontaminated runs, which did not differ. This increased variability may reflect fluctuations in recruitment of proactive control and cue monitoring in this more demanding task. Increased σ has been observed in children with and without attention deficit hyperactivity disorder (ADHD) when the complexity of a go/no-go inhibitory control task was increased (Vaurio et al., 2009). Sigma is also increased in ADHD versus typically developing children, which has been interpreted as reflecting impaired response preparation (Vaurio et al., 2009). In contrast, τ was increased in the contaminated runs, but not sensitive to cue salience, and not associated with transient BOLD changes. The greater frequency of slower RTs may be related to transient increases in periodical checking (Scullin et al., 2013; Gynn, 2003) or the fact that participants needed extra time on ambiguous trials to check whether the position of the two shapes matched a chess knight's move. Tau has also been associated with lapses in attention both in children (Vaurio et al., 2009) and in adults with ADHD (Gmehlin et al., 2014). These ex-Gaussian analyses suggest that a variety of mechanisms, related to proactive anticipation, lapses in attention, and reactive processes triggered by the cue, are underlying differences in RT between uncontaminated and PM runs varying in PM cue salience.

PM Execution (PM Trials)

Participants were slower and less accurate for PM trials than OT trials, in line with similar performance differences observed by Simons et al. (2006). This pattern is consistent with the additional demands of PM trials including cue identification, intention retrieval, inhibition of the OT, and branching into subtasks necessary for successful performance. The slowing down observed for OT trials in the Knight run relative to the Color run was larger for PM trials; that is, participants were relatively slower to respond to nonsalient PM cues than salient PM cues. There was no difference in accuracy. The current results align with reports of strong influence of cue manipulations on PM (Kliegel et al., 2013; McGann, Ellis, & Milne, 2002). For example, high PM cue salience has been demonstrated to enhance PM in younger adults (Einstein et al., 2005;

Brandimonte & Passolunghi, 1994; Einstein & McDaniel, 1990), older adults (Altgassen et al., 2010), and children (Kliegel et al., 2013). Overall, our results are consistent with the well-documented facilitation effect of salient cues and suggest that a variety of cognitive mechanisms underlie this effect, including strategic monitoring as well as spontaneous retrieval.

Across age groups, PM accuracy was negatively correlated with PRMQ (PM), which assesses PM failures in daily life (Smith et al., 2000). Similarly, PM accuracy was negatively correlated with WebExec, indicating that more executive function failures were associated with lower PM accuracy. Although these exploratory correlation analyses would need to be replicated in a larger sample, our results suggest that general executive functioning might be an important individual trait associated with PM performance, as has been reported in adolescents (Robey, Buckingham-Howes, Salmeron, Black, & Riggins, 2014) and adults (Gonneaud et al., 2011).

Adolescent Performance

Adolescents were overall less accurate on the task, on both OT and PM trials, and had a greater frequency of particularly slow responses, as is indicated by higher τ in OT trials across conditions. These results were mostly driven by the younger adolescents in the sample. Combined, these results may reflect lapses in attention leading to a higher frequency of slower RTs and a higher frequency of errors in adolescents than in adults. This is consistent with findings that sustained attention continues to improve during adolescence (Brocki & Bohlin, 2004).

Focusing on OT trials, our results showed that adolescents and adults showed similar patterns of RT costs related to the maintenance of the PM intention and PM cue salience effects on RT. These results suggest that the capacity to flexibly engage proactive and reactive control to maintain PM intentions and monitor for salient versus nonsalient PM cues is similar in adolescents than in adults. High PM cue salience has been demonstrated to enhance PM in preschool (Kliegel et al., 2013) and school-aged (Mahy et al., 2014) children as well as in young and older adults (Altgassen et al., 2010; Brandimonte & Passolunghi, 1994; Einstein & McDaniel, 1990). Here, we demonstrate similar enhancement effects of salient cues for both adolescents and adults. Contrary to our hypothesis, the interaction between cue salience and age was not significant. Thus, the current study appears to suggest that there may be similar facilitation mechanisms driven by cue salience across adolescence and into adulthood. In line with results in children (Kliegel et al., 2013), cue salience might not be the key mechanism underlying PM development.

Previous studies did observe age differences in OT performance. For example, lower accuracy in a contaminated OT was reported in adolescents (13–16 years old) compared to adults when the OT had high, but not low, cognitive demand (Ward et al., 2005). Similarly, 12- to 13-year-olds

and 14- to 15-year-olds had lower accuracy than 18- to 19-year-olds in a contaminated ongoing lexical decision task, where 12- to 13-year-olds were also slower than other age groups (Bowman et al., 2015). Exploratory analyses across the adolescent age range indicated that accuracy, but not RT, increased linearly with age in the contaminated runs. Integrating the results of this study to previous research suggests that differences in performance on contaminated OT trials between adolescents and adults may only be observed when the demands of the OT are high. Such a pattern of greater developmental differences in most challenging conditions has been observed, for example, in working memory tasks with greater developmental differences for greater working memory loads (De Luca et al., 2003).

Looking at PM trial performance, again, effects of cue salience on PM trials' RT were similar in adolescents and adults. However, across cue salience conditions, adolescents, and specifically younger adolescents aged 12–14 years, showed lower accuracy and slower RT in PM trials, relative to OT trials. Previous studies investigating differences in PM performance between adolescents and adults have found mixed findings. There have been reports of increased PM performance with age between adolescence and adulthood in terms of accuracy (Altgassen et al., 2014; Wang et al., 2006, 2011; Zöllig et al., 2007) and RTs (Bowman et al., 2015), but also of improvements between childhood and adolescence, with no further maturation of PM after adolescence, especially for focal cues (Zimmermann & Meier, 2006; Ward et al., 2005), and particularly after the age of 13 years (Bowman et al., 2015). Our results are broadly in line with this literature and suggest that adult PM performance is reached in midadolescence.

PM and OT performance are usually not directly compared in other developmental studies. Although PM and OT trials are not directly equivalent, we believe comparing PM trial performance to OT trials may be useful to distinguish between general (e.g., changes in processing speed) and PM-specific improvements with age and suggest that future studies could benefit from including this analysis. We did not find differences in self-reported PM failures in real-life settings between adolescents and adults. However, to our knowledge, the PRMQ has only been used in adult populations in the past (Smith et al., 2000). Although the PRMQ was piloted in adolescent participants, and the questions were screened for age appropriateness, further studies could more systematically investigate how suitable the PRMQ is to detect developmental differences. There was a trend for adolescents to score lower in the FOS compared to adults. These results are in the direction of the pattern typically observed in the literature (Steinberg et al., 2009), in which adults are more oriented toward the future than adolescents.

Differences in executive functioning (forward and backward digits span, no-go accuracy) and future orientation were found to partially explain nonspecific RT differences

between adolescents and adults on Contaminated runs across OT and PM trials. However, age group differences in accuracy and specific differences in RT and accuracy on PM compared to OT trials between adolescents and adults remained significant when accounting for these variables, suggesting that there are specific mechanisms of PM that are still maturing, independent of the maturation of working memory, inhibitory control, and future orientation.

Neuroimaging Findings

Sustained Changes in BOLD Signal:

PM Intention Maintenance

Intention maintenance was associated with sustained activity in regions implicated in PM, with activation in similar regions, but to varying strength, for salient and nonsalient PM cue conditions. The current findings are robustly aligned with reports of regions that respond in a sustained fashion in PM task blocks, notably RLPFC, DLPFC, ACC, and inferior parietal lobe (McDaniel, Umanath, Einstein, & Waldum, 2015; McDaniel et al., 2013; Reynolds, West, & Braver, 2009). Administration of PM instructions, which leads to the maintenance of an internal representation of the delayed intention as well as cue monitoring, was associated with sustained higher BOLD signal in the right rostral aspects of the lateral pFC, including BA 46 and extending into BA 10, the key region implicated in PM (Momennejad & Haynes, 2012; Gilbert et al., 2006; Simons et al., 2006; Burgess et al., 2003).

In addition, there was activation of ACC and of the DLPFC (BA 46) extending into superior frontal cortex (BA 44) as well as VLPFC (BA 47/45). These results are in line with the increased recognition of involvement of more extended frontoparietal networks in PM processes (Cona et al., 2015; McDaniel et al., 2013). The anterior insula was also recruited in both hemispheres. Activity in these regions has been reported in other PM studies in nonfocal tasks (Beck et al., 2014; Rea et al., 2011; Gilbert et al., 2006, 2009; Burgess, Quayle, & Frith, 2001) suggesting a role of the anterior insula in cue monitoring (Cona et al., 2015; McDaniel et al., 2015). Overall, and in line with previous accounts, activation of DLPFC, bilateral anterior insula, and superior parietal lobule may relate to preparatory processes that include maintaining the task set (e.g., instructions for PM trials) in anticipation of cues to enable goal pursuit in the DMC framework (Magis-Weinberg et al., 2019; Jiang et al., 2015; Braver, 2012).

There was considerable overlap in neuroimaging results between the salient and nonsalient PM cue conditions, consistent with behavioral evidence of interference costs in both runs. However, contamination with nonsalient cues did recruit more extensive regions overall. There were greater increases in BOLD signal during OT Knight run than OT Color run blocks in the superior parietal

lobules bilaterally (BA 7 and BA 40), a region that has been implicated in encoding and maintenance/retrieval of PM intentions (Gilbert, 2011; Poppenk, Moscovitch, McIntosh, Ozcelik, & Craik, 2010; Reynolds et al., 2009). The reverse contrast revealed a set of regions, namely, the angular gyri, superior frontal gyrus, and midcingulate cortex, which showed greater decreases in BOLD signal during OT Knight run than OT Color run blocks. These regions are typically considered as part of the default mode network, which shows decreases in BOLD signal when task demands increase (Raichle, 2015), which fits with the results observed here. We did not find an association between either PRMQ or FOS and average activity in contaminated runs across cue salience.

Transient Changes in BOLD Signal: PM Trial Execution

The RLPFC exhibited transient changes in BOLD signal during PM trials, as has been described in previous fMRI studies, which have reported higher activity in RLPFC when participants either anticipate or encounter PM cues (Reynolds et al., 2009; Simons et al., 2006; Burgess et al., 2003). Additional transient activation for salient and nonsalient PM trials was observed in ACC, bilateral anterior insula, precentral gyrus, middle frontal gyri, and superior parietal lobe, results that are in line with transient activations in a nonfocal PM task that investigated proactive and reactive strategies (McDaniel et al., 2013). Along with activity in VLPFC (BA 45) and anterior insula (BA 47), these results might speak to the involvement of bottom-up attentional processes captured externally by the PM cue (Cona et al., 2015).

While Knight PM trials overall seemed to elicit more widespread changes in BOLD signal than Color PM trials, no significant differences emerged, which may reflect that, although the PM cues differed, the PM intention (pressing the thumb button) was the same for both. These results are in contrast with the behavioral findings of slower RTs in Knight PM trials than Color PM trials. Importantly, however, OT trials served as a baseline for these contrasts, and RTs were also slower in Knight OT trials than Color OT trials. Although this difference was greater in PM trials, this was by only 58 msec, a difference unlikely to be picked up by fMRI measures of neural activity. Overall, these results indicate that cue salience was associated with differences in sustained activation, with greater sustained activation in the low-cue-salience condition in the right superior frontal gyrus and bilateral superior and inferior parietal lobules, but cue salience did not impact transient changes in activation associated with PM trials.

The left anterior insula, right superior parietal lobule, DLPFC, precentral gyri, and FEFs, as well as middle aspect of ACC, exhibited a mixed pattern of sustained and transient differences in BOLD signal as a function of the PM context or PM trial execution. The anterior insula has been found to show sustained and transient changes in a PM task (Cona et al., 2015; Gilbert et al., 2009), suggestive of a role both

in sustained task control and in increasing the salience of the cue (Cona et al., 2015). McDaniel et al. (2013) also found a mixed pattern of activation in the precentral gyrus (BA 44) and FEF in the middle frontal gyrus (BA 6) for a nonfocal PM task. More generally, these regions have been implicated as neural correlates of the DMC (Magis-Weinberg et al., 2019; Jiang et al., 2015), where temporal dynamic within some regions, in addition to activation of distinct brain networks, would enable the shift between modes of proactive and reactive cognitive control. The anterior insula has been suggested to monitor current control demands and sustain task control, and rostral ACC reactively monitors level of conflict and then signals DLPFC and dorsal ACC to mediate trial-by-trial conflict-driven adjustments in control (Magis-Weinberg et al., 2019; Jiang et al., 2015). When PM cues are detected, conflict may arise between the goal of continuing to perform the OT and the retrieval of the relevant PM intention followed by execution of the PM response, giving rise to transient activity during PM trial (Hashimoto, Umeda, & Kojima, 2011).

Age-related Differences

No differences were observed in the planned analyses comparing sustained and transient BOLD signal changes between adolescents (12–17 years old) and adults (23–31 years old). Given that developmental investigations of PM using fMRI are limited, we further explored age differences between younger adolescents, older adolescents, and adults. Age differences emerged for PM trials in which younger adolescents had higher transient BOLD signal in occipital regions than adults, with no differences with the older adolescents. These results indicate that, overall, adolescents recruit similar brain networks to adults and, to a similar extent, during event-related PM tasks, which is in line with the mostly similar behavioral correlates of PM observed between the two age groups in this study. The finding with the younger adolescents is consistent with the behavioral results of the current study, which revealed that younger, but not older, adolescents showed lower accuracy and slower RTs in PM trials relative to OT trials than adults, as well as with previous research suggesting that PM performance stabilizes by midadolescence, around 13–14 years old (Bowman et al., 2015; Zimmermann & Meier, 2006; Ward et al., 2005). Although we expected to observe differences in pFC functioning, possibly in the RLPFC, a region that has consistently been associated with PM and that continues to mature during adolescence (Dumontheil, 2014), we instead found increased recruitment of posterior regions in younger adolescents, in addition to commonly recruited brain regions, as has been observed in a go/no-go task (Jonkman, Sniedt, & Kemner, 2007). In this case, the results were interpreted as reflecting the fact that younger children may bolster their performance with basic stimulus processing and attention mechanisms. A study in adults found that occipital areas show greater activation

during event-based than time-based PM, and this was interpreted as reflecting target-checking (Gonneaud et al., 2014). Our results may therefore suggest that younger adolescents engaged in more extensive target-checking.

Limitations and Future Directions

PM tasks are also dual-task paradigms that require participants to execute the OT and the PM task in parallel. In this view, behavioral and neural correlates of PM tasks might be reflecting general dual-task demands and associated cognitive processes (Dumontheil, 2014). There is also a cognitive branching component (Hyafil, Summerfield, & Koehlin, 2009), in which participants disengage momentarily from the OT and switch to the internal representation of the PM intention. These explanations are in line with other proposed interpretations of RLPFC function (Koehlin, 2016), and ultimately, PM processes cannot be entirely dissociated from branching performance processes with the current design.

There was evidence for strategic monitoring for both salient and nonsalient cues. This might be because the current paradigm employed a nonfocal PM task, which has been shown to elicit strategic monitoring in previous studies (see McDaniel et al., 2015, for a review). Alternatively, as has been identified by McDaniel et al. (2015), isolating spontaneous retrieval is difficult in traditional laboratory settings. Contextual factors in the way experiments are set up and delivered might encourage monitoring even with focal cues. Monitoring that responds to instruction framing or a high number of PM target cues could mask discovery of bottom-up spontaneous retrieval processes.

Exploratory analyses comparing the youngest with the oldest adolescents and adults hinted at maturation of PM in early adolescence. Accuracy, but not RT, increased linearly with age in the adolescent group. Our sample size, however, might limit our ability to detect age-related changes. To fully capture age-related differences, future studies should include a larger number of participants and sample across a wider age range to include late childhood. In the current task, it seems that varying cue salience did not require high enough levels of monitoring that developmental differences were apparent. To further understand which aspects of controlled processes are targeted by cue salience during adolescence, it might be important to systematically manipulate complexity and cognitive demands. In addition, manipulations around cue salience that align with adolescent sensitivities (such as socioemotional processes) might be an interesting route going forward, especially because positively valenced cues have been shown to improve PM in adults (Hostler, Wood, & Armitage, 2018; Altgassen et al., 2010).

Conclusion

Our results show that, when intention retrieval demands are matched, PM cue salience modulates performance

and sustained activation during the OT. Whereas accuracy did not vary as a function of cue salience, the low-cue-salience PM condition was associated with slower RTs, with a shift in the mean distribution of RT, and greater sustained activation in the right superior frontal gyrus and bilateral superior and inferior parietal lobules. We add to the nascent body of literature of neural markers of different strategies, in the proactive/reactive control framework, in relation to maintaining intentions and task retrieval. We show that, beyond the recruitment of regions typically implicated in PM, such as the RLPFC, regions that are typically associated with proactive control are recruited for intention maintenance, for both adolescents and adults. We found that neural correlates of PM trials were not specifically modulated by cue salience, revealing little difference in reactive control between conditions. These results underscore how retrieval and cue detection are separate processes that map onto different cognitive control strategies. Finally, we show, for the first time, that adolescents and adults share similar modulation of performance and neural activity by cue salience. However, the younger adolescents showed specifically lower accuracy and slower RTs on PM trials, as well as increased activation in a posterior occipitotemporal cluster, providing evidence that PM maturation continues during early adolescence.

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Note

1. In the scanner, participants completed the shapes task after the administration of two 8-min runs of a working memory and reward task, for an unrelated study (Magis-Weinberg et al., 2019). Associated with the working memory and reward task study, participants completed computerized versions of the Behavioural Activation Scale (Carver & White, 1994) and Sensitivity to Punishment and Sensitivity to Reward Questionnaire (Torrubia, Ávila, Moltó, & Caseras, 2001).

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