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# Default-mode network activation underlies accurate contextual processing of exclusive disjunctions in older but not younger adults

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ABSTRACT

Young adults proactively engage frontoparietal processing of contextual cues to preempt subsequent events. Rather than being preemptive, older adults engage these brain areas reactively upon event occurrences. Reactive frontoparietal processes in older adults, however, might be insufficient for complex contextual neural computations where utilities of contexts are not straightforward but dependent on a set of stimulus-response rules. Applying non-linear logic (XOR) rules in an fMRI experiment, we found higher default-mode network (DMN) activity critical for correctly responding to such contingency in older but not younger adults. Moreover, older individuals with higher proactive cue processing showed better performances with less DMN activity. Thus, DMN processing provides critical support when older adults are faced with complex contextual contingencies. These findings suggest an age-related change in the neurocomputational role of introspective processes in decision-making from young to older adulthood.

## 1. Introduction

Findings from functional neuroimaging studies suggest that young and older adults engage different cognitive strategies to integrate contextual information for task performance (Braver, 2012; Grady, 2012; Schoenbaum et al., 2002; Schoenfeld, 2014; Weiler et al., 2008). Young adults evince frontoparietal activity associated with proactive processing of contextual cues or task goals during cue-probe (Paxton et al., 2008) and task switching (Jimura and Braver, 2009) experiments. By contrast, in the same tasks older adults engage neural responses that reflects a more reactive strategy, showing higher neural activity during probes and less processing of preceding cues. Intriguingly, despite these age differences in cue- and probe-related neural engagement, reactive processing appears to be sufficient for older adults to show comparable behavioral performances to young adults in the above studies. Thus, it is of interest to know more specifically how such differential neural information processes operate in young and older adults when solving contextual problems given age-related differences in proactive and reactive strategies. Moreover, there is a need to determine the extent to which such preservation of performance with age, subserved by these strategic neurocomputational differences, applies across different types of contextual problems.

Contextual processing studies commonly apply AX-CPT (AX continuous performance task;Cohen et al., 1999; Servan-Schreiber et al., 1996) or similar paradigms in which participants view stimuli sequences (e.g. letters) and are required to make target responses only to X probes when the preceding cue is A (AX events), but non-target responses to all other stimuli (A- and B-cues, and AY, BX, and BY probes). Based on such contingency, it is difficult to distinguish whether neural responses characterizing reactive processing of probes in older adults stem from post-hoc processing of past contextual cues after seeing the probe (e.g. retrieving A- or B-cue), or from inhibition of target responses associated with the target probe (e.g. suppressing X or Y probe responses). Critically, such cue-probe response mapping rules as assessed in AX-CPT or similar paradigms are linearly separable (i.e. solvable using one single rule such as making a target response when seeing AX). As a result, it remains unclear how neural processing under a reactive strategy operates in older adults to solve problems that require more complex rule integration (e.g. applying two contingent rules such as making the same target response when seeing either AX or BY), which might be more common in real life.

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In this present study, we evaluated how different contextual processing strategies in young and older adults engage distinct neural network operations for accurate behavioral decisions that involve exclusive disjunctive rules governing responses to cue-probe pairs. We borrowed from the modified symbolic version of AX-CPT, the Dot Probe Expectancy task (DPX; Jones et al., 2010; Lopez-Garcia et al., 2016), and built the XDPX paradigm, which incorporates XOR logic in the cue-probe response rules (Fig. 1). In XDPX, participants make target probe responses to AX as well as BY trials so that the rules governing cue-probe mappings are no longer linearly separable (Minsky and Papert, 1969). In addition, there is higher presentation frequency of AX trials such that a prepotency of stimulus-response mapping is established for this condition. Comparing AX with the AY condition, which shares the same cue but requires a different probe response, evaluates neural processes involved in basic inhibitory control of prepotent responses. Comparing BX and BY conditions relative to AX baseline condition reveals cognitive control processes involved in integrating cue-probe information over multiple levels of rules, i.e. rules associated with the current probe that is online given the rules associated with the cue just encountered.

We considered that both proactive and reactive strategies in young and older adults, respectively, must integrate the same basic contextual information for appropriate selection of response contingencies. Proactive processing of contextual cues, however, theoretically affords preemptive selection of a set of potential responses based on task rules during cues to filter and reduce subsequent competition between different response rules during probes (Braver, 2012). Thus, for complex contextual problems as in the XDPX, such predictive processing effectively parses the non-linear rule into two simpler linear associations (i.e. select A- or B-cue rule set first, then apply selected rule set upon X- or Y-probe onsets). By contrast, in reactive processing, cue information is accessed in-depth only when probes are presented. Such contextual processing involves less predictive filtering of rule sets based on cues and rely on attentional (to detect AX events) and inhibitory control (to inhibit prepotency in AY trials) during probes, processes that might be sufficient for linear mappings. When it comes to non-linear rule mappings, however, a reactive strategy should also require additional neural processing during probes that involves retrospective retrieval of cue-related information as well as reconciling cue-probe response mappings that have yet to be resolved at the time of the probe (i.e. whether to apply AX, AY rules or BX, BY rules).

Enhanced *activation* of default-mode network (DMN) brain areas has been shown to facilitate performance on tasks requiring retrospection of stored mnemonic representations (Konishi et al., 2015; Spreng et al., 2010, 2014). Note, DMN responses are typically deactivated (lower than rest baseline) during task trials and more active during self-related processing (Andrews-Hanna et al., 2014; Buckner et al., 2008; Dixon et al., 2014; Orr and Banich, 2014; Raichle, 2015). Such response patterns suggest that the DMN is involved in introspective and retrospective retrieval processing, which are engaged during rest periods or during access to internal mental representations of information not currently arising from upstream sensory processing. Studies have reported older adults show less *deactivation* of the DMN than younger adults during rest periods in cognitive tasks (Andrews-Hanna et al., 2007; Damoiseaux et al., 2007; Grady et al., 2009; Park et al., 2010; Persson et al., 2007; Sambataro et al., 2010; Spreng et al., 2016; Turner and Spreng, 2015), which is interpreted to reflect age-related reduction in suppression of irrelevant introspective processing. We hypothesized, however, that DMN processing in older adults is critical for accurate decision behavior given a reactive strategy for non-linear problems that requires retrospective integration of cue-probe information over multiple levels of rules. In particular, DMN operations might be a means for older adults to solve non-linear contextual problems in which simply enhancing attention or inhibitory processes in other brain regions are insufficient to meet task demands (see Spreng and Turner, 2019, for a review on this notion).

Therefore, using the XDPX task in a functional brain imaging experiment, we evaluated the effect of age differences in contextual processing strategy, as indicated by their neural correlates, on the correct (vs. incorrect) selection of non-linear cue-probe response rules. As in past studies, we expected lateral frontoparietal responses to be greater in younger than older adults during cue stimuli consistent with more proactive processing of task rules in anticipation of probes (Braver and West, 2008) as well as the involvement of these brain regions in task rule selection and goal maintenance (Digirolamo et al., 2001; Lopez-Garcia et al., 2016; Macdonald et al., 2000; Paxton et al., 2008). Also as in past studies, we expected higher frontoparietal probe responses in older than younger adults in line with more reactive attention and inhibitory control operations during probes given reduced processing of cues. Critically, higher DMN *activity* during BX and BY probes should be required for correct (vs. incorrect) responses in older but not younger adults. In addition, older neural responses during BX and BY probes should have distinct correlation patterns with individual correct behavioral performance compared to AY probes. This is because the latter involves inhibition of prepotent responses whereas the former additionally involves retrospective retrieval of cue-probe rules. Specifically, for a reactive strategy, higher neural responses engaged during AY probes should be associated with faster successful inhibition of prepotent responses. By contrast, higher neural responses reflecting reactive retrospective retrieval should be associated with slower contextual integration during correct BX and BY responses. Finally, we expected that older individuals who engage more proactive neural processing of cues should therefore engage less reactive neural processing of probes and evince more young-like contextual processing behavior as well.

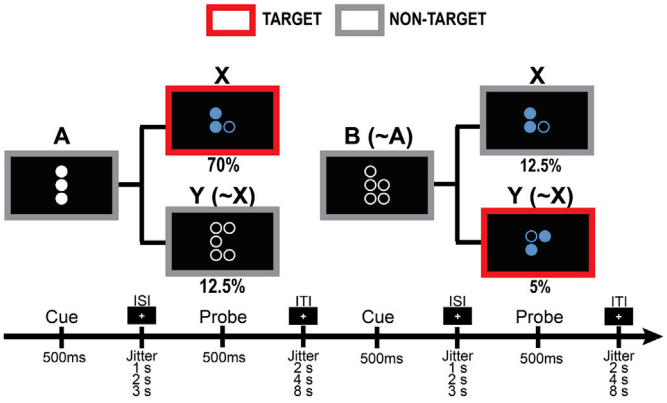


**Fig. 1. The XDPX paradigm.** Two fixed symbols were assigned as the A cue and the X probe as shown above. All non-A cues are collectively B cues, and all non-X probes are collectively Y probes. Cue-probe pairings comprised four trial types: AX, AY, BX and BY, with frequency of occurrences 70%, 12.5%, 12.5%, and 5%, respectively. Probes requiring target responses are shown in red borders, and probes requiring non-target responses in grey borders. The task stimulus-response rule follows an X-OR logic table. Stimulus duration (SD) = 500 ms; Inter-stimulus interval (ISI) ranged between 1s, 2s, and 3s (mean = 2s); Inter-trial interval (ITI) ranged between 2s, 4s, and 8s (mean = 4s).

## 2. Materials and methods

### 2.1. Participants

Twenty-six younger and 30 older adults completed the fMRI XDPX experiment as well as a neuropsychological test battery. Participants were recruited through online and local community advertisements and were screened for presence or history of neurological and psychiatric disorders, artificial implants, and other counter-indications for MRI scanning. All participants were right-handed and used corrected vision as necessary in the scanner. Written informed consent was obtained from all participants for this study, which was approved by the National Taiwan University Hospital Research Ethics Committee. One young and four

older adults were excluded from data analysis due to excessive head movement during functional imaging (>3 mm translation or > 3° rotation; based on the size of one functional voxel). One young adult fell asleep during the task. One young and seven older adults had no correct trial in at least one task condition during either training phase or inside the scanner and were excluded from further analyses (see below). The remaining 42 participants consisted of 23 healthy young adults (13 female) aged between 20 and 29 yrs (mean age = 24.13 yrs, SD = 2.49 yrs) and 19 older healthy adults (13 female) aged between 62 and 78 yrs (mean age = 69.79 yrs, SD = 4.20 yrs). All older adults in this analyzed sample scored >26 on the Mini Mental State Examination (MMSE).

### 2.2. XDPX stimuli and procedures

Thirteen Braille symbol stimuli were downloaded from the Cognitive Neuroscience Test Reliability and Clinical applications for Schizophrenia (CNTRACs) Consortium website (http://cntracs.ucdavis.edu). The experimental paradigm is shown in Fig. 1. One fixed symbol was assigned as the A-cue and another the X-probe. The 11 other symbols were used as B-cues (non-A-cues) and Y-probes (non-X-probes). A single trial consists of one cue and one probe. Combinations of these stimuli then comprised the 200 cue-probe pairs (trials) in the fMRI experiment, of which 140 were baseline AX (70%), 25 were AY (12.5%), 25 were BX (12.5%), and 10 were BY (5%). Note that under this distribution, BX relative to other trial types should be more difficult to inhibit due to the established AX response prepotency. By contrast, BY relative to other trial types should involve more retrospective contextual processing because both cue and probe are non-fixed stimuli.

All participants underwent a training session prior to entering the scanner. In the training, participants were first instructed to make target responses to the X-probe if it was preceded by the A-cue and to Y-probes (non-X-probes) preceded by B-cues (non-A-cues), and to make non-target responses for all other stimuli, as depicted in red squares in Fig. 1. Participants then performed an orientation phase using sample card stimuli with vocal responses, without prepotencies imposed, and without time constraint. Participants who had no correct responses in at least one condition were deemed not to have understood the task rule and repeated the orientation phase until criterion. Participants who met orientation criterion performed a familiarization phase on the computer with the same ratio of conditions, stimulus duration, and jittered inter-stimulus (ISI; the time between cue and probe) and inter-trial intervals (ITI; the time between cue-probe trials) as the fMRI experiment. Again, participants repeated the familiarization phase if they did not meet the above criterion. Because our analysis requires distinctions to be made between correctly and incorrectly responded trials in task conditions, participants who did not provide any correct trial in at least one condition during training or the fMRI experiment were excluded from further analysis.

For the fMRI experiment in the scanner, stimuli were presented using E-Prime software version 2.0 (Psychology Software Tools, 2016) and back-projected onto a screen at the rostral end of the scanner, which participants viewed through a mirror mounted on the head coil. There were five functional runs of the XDPX task, each lasting 5 min and consisting of 40 cue-probe trials. Twenty-second fixation intervals were presented in the beginning and the end of each run to facilitate baseline functional signal estimation. Stimuli duration was 500 ms with a 1500 ms response window. ISIs ranged between 1, 2, and 3 s (mean = 2 s) and ITIs between 2, 4, and 8 s (mean = 4 s). Stimuli were presented in pseudo-random order so that no stimulus and no condition trial type (except for the AX condition) were repeated more than 2 times consecutively.

### 2.3. Power analysis

Because no previous studies have used the XDPX task, we estimated power and sizes of the effects of age based on related measures available using G*power software ver. 3.1.9.4 (http://www.gpower.hhu.de; Faul et al., 2007; Faul et al., 2009). For behavioral accuracy, we considered the letter-sequence AX-CPT AY condition error rate that showed significant age differences in Rush et al. (2006). The behavioral age effect size estimated was 0.768 (Young: mean (SD) = 13 (15) %; Old: mean (SD) = 4 (7) %; Table 2 in that study), which projects a sample size of 22 in each age group to obtain a type I error ($\alpha$) of 0.05 at a power ($1 - \beta$) of 0.80. Applying this in our sample of 23 young vs. 19 old at $\alpha = 0.05$, we estimated a power of 0.785 to detect significant age differences in behavioral accuracy. Rush et al. (2006) also showed a significant age difference in BX response times with an effect size of 1.214 (Young: mean (SD) = 374 (112) ms; Old: mean (SD) = 576 (206) ms; Table 2 in that study), projecting a sample size of 12 in each age group at $\alpha = 0.05$ and $1 - \beta = 0.80$. For task-related functional neural responses, we considered Paxton et al., 2008 (Study 2) which found significant higher probe-related responses with age in whole-brain contrasts in a letter-sequence AX-CPT task. Information on neural response variability were not accessible from that study, preventing an estimate of effect size. Nevertheless, we note the sample for their significant whole-brain results included 16 young and 16 older adults. Finally, for default-mode network (DMN) responses, we considered Turner and Spreng (2015) which reported significant age differences in DMN activity during an executive control task. Because the Tower-of-London task used in that study was quite distinct from our XDPX task, we were unable to obtain a relevant *a priori* effect size for neural responses. Nevertheless, we note that that study found significant age effects in DMN responses during an executive control task using 18 young and 18 older adults. Taken together, we considered that our final sample of 23 young and 19 older adults, selected out of the original full sample of 26 young and 30 older adults based on better performance, had comparable power as previous studies to detect our targeted behavioral and neural effects.

### 2.4. Behavioral analyses

Behavioral task performances were submitted to regression analyses using the lme4 package (Bates et al., 2015) under the R environment (R Core Team, 2017). Trials with incorrect cue responses were excluded from all analyses as dummies (for both A- and B-cue, the correct responses are always "non-target"). Probe response accuracies (proportion of correct or incorrect binary responses) were analyzed using a generalized linear mixed model with a logit link function while correct and incorrect response reaction times were analyzed using linear mixed models. Both models included age group (young, old), trial type condition (AX, AY, BX, BY) and their interactions as fixed effects and subject as a random effect to account for individual differences in performance. Variables were dummy coded with young adults treated as the intercept for age group, baseline AX treated as the intercept for condition trial type, and young adult*AX treated as the intercept for the interaction effect of age by trial type.

### 2.5. Brain imaging protocol

Brain imaging data were acquired on a 3T Siemens MAGNETOM® Skyra scanner (Siemens Healthcare, Erlangen, Germany) located at the Taiwan Mind and Brain Imaging Center, National Cheng-Chi University, Taipei, Taiwan, with a 32-channel head coil. Functional runs used an echo-planar imaging (EPI) sequence with 38 axial 4 mm slices parallel to the anterior-posterior commissural plane, repetition time (TR) = 2 s, echo time (TE) = 24 ms, flip-angle (FA) = 90°, in-plane matrix size = 64 × 64, field of view (FOV) = 220 × 220 mm, 150 vol/run. T2 scans coplanar to the EPI images were also acquired for coregistration with TR = 7480 ms, TE = 102 ms, FA = 150°, 256 × 256 matrix, FOV 256 × 256 mm, 38 axial 4 mm slices. Finally, T1 magnetization prepared rapid acquisition gradient echo (MPRAGE) images were acquired for spatial normalization with TR = 2 s, TE = 2.98 ms, FA = 9°, 192 sagittal 1 mm slices, 256 × 256 matrix, FOV 256 × 256 mm.

### 2.6. Functional whole-brain image analysis

Functional images were preprocessed using SPM12 (Statistical Parametric Mapping, Wellcome Trust Centre for Neuroimaging, UK). Functional images were first corrected for slice-time acquisition and motion. T2 anatomical images were coregistered to the functional images, and T1 images to the coregistered T2 images. To minimize the effect of aging on brain structure, T1 images were segmented and submitted to the Diffeomorphic Anatomical Registration Through Exponentiated Linear Algebra procedure (DARTEL) to create a study-specific template (Ashburner, 2007), with the parameters applied to functional images. Normalized functional images were resampled to $3 \times 3 \times 3$ mm voxel sizes and smoothed with an 8 mm 3D Gaussian kernel.

For each participant, we applied a first-level whole-brain voxel-wise analysis on preprocessed functional images. This analysis used a general linear model (GLM) based on onset regressors for the cues (correct-response A-cue and B-cue), probes (correct-response probes for AX, AY, BX, and BY trials separately, and incorrect-response probes for AY, BX, and BY trials separately), and dummy trials (null-response, incorrect cue-response and AX incorrect probe trials). Onset regressors were convolved with the canonical hemodynamic response function (HRF). Six movement parameters were also included as head-motion covariates resulting in a total number of 80 regressors in the first-level GLM (16 regressors for each of the five runs). Whole-brain contrasts images of mean response parameter estimates across runs for the cue and probe conditions were then obtained and fed into the second-level group analysis.

For group-level voxel-wise analysis, planned contrasts were conducted to evaluate specific age differences in whole-brain responses to cues and probes. For cues, we expected that neural responses to the infrequent contextual cues would be higher than to the frequent cues and that such proactive processing of cues should be reduced with age. Thus, we examined the contrast [B-cue – A-cue] separately in young and old, as well as $[\text{B-cue} - \text{A-cue}]_{\text{Young}} - [\text{B-cue} - \text{A-cue}]_{\text{Old}}$ to identify brain areas where cue response differences were greater in young than older adults.

For probes under the A-cue context, we expected that older adults would require greater neural resources than younger adults when inhibiting prepotent cue-probe mappings that were established through the most frequent AX trial type. Thus, we examined significant brain areas in the contrast [AY – AX] separately in young and old, as well as $[\text{AY} - \text{AX}]_{\text{Old}} - [\text{AY} - \text{AX}]_{\text{Young}}$, for correct trials only. For probes under the B-cue context, we expected that reactive processing of probes in older adults should involve additional retrospective contextual cue retrieval, and thus higher neural activity, compared to probe processing based on a proactive strategy in younger adults. As such, we first examined [0.5*[BX + BY] – AX] separately in young and old, as well as $[0.5*[\text{BX} + \text{BY}] - \text{AX}]_{\text{Old}} - [0.5*[\text{BX} + \text{BY}] - \text{AX}]_{\text{Young}}$, for correct trials only. Note that in this case we subtracted out the AX probe from the B-cue probe responses to account for base age differences in brain activity during probe processing. To dissociate brain responses necessary for successful probe response behavior in each group, we further compared contrasts between correctly and incorrectly responded trials for both A-cue and B-cue probes. Finally, to dissociate brain areas differentially sensitive to age differences in inhibition of prepotent responses to X-probes vs. retrospective retrieval for Y-probes under B-cue contexts, we evaluated the contrast [BY – BX] separately in young and old, as well as $[\text{BY} - \text{BX}]_{\text{Old}} - [\text{BY} - \text{BX}]_{\text{Young}}$, for correct trials only.

Whole-brain statistical map significance voxel threshold was set at $p < 0.001$, with cluster size of at least 48 contiguously significant voxels. This criterion was determined using AlphaSim in the RESTplus toolkit version 1.2 (http://restfmri.net/forum/RESTplusV1.2; Song et al., 2011; see also Cox et al., 2017) that performed Monte Carlo simulation with 10,000 iterations and fulfilled a whole-brain cluster-wise family-wise error (FWE) rate of $p < 0.05$. Thus, using this criteria, the probability of falsely detecting a significant cluster in any given whole-brain contrast in our data analysis is $p < 0.05$.

### 2.7. Functional regions-of-interest (ROI) analysis

Functional response estimates were extracted from ROIs defined based on the planned whole-brain contrasts (as described accordingly in each section of the results) to investigate neural responses across cue and probe conditions as well as age differences in greater detail, and to examine associations with behavioral performance. ROIs were contiguously significant voxels within 8 mm-radius spheres centered on peak activation voxel coordinates based on the corresponding functional contrasts. Neural response parameter estimates of relevant conditions were then extracted from each ROI for each participant and used in external statistical analysis or evaluation against behavioral performance. Associations between ROI brain responses and behavior were only considered significant at false discovery rate (FDR) adjusted $p < 0.05$ due to multiple comparisons across ROIs. To account for possible issues due to small sample size, Hedges' g and Cohen's d (adjusted for small sample size) for group and condition effects, respectively, were also calculated to show effect sizes for ROI-related results (Cohen, 1992, 2013; Durlak, 2009; Sawilowsky, 2009). Briefly, effect sizes at 0.2, 0.5, 0.8, to 1.2 are considered small, medium, large, to very large effects, respectively. Correlation analyses were calculated using Pearson's r with coefficients at 0.5 considered large effects.

## 3. Results

### 3.1. Accuracy for B-cue conditions lower in old than young

Age group (young and older) and individual mean response accuracies (number of correct response trials divided by number of all responded trials) and mean reaction times for correct and incorrect trials across the AX, AY, BX, and BY conditions are plotted in Fig. 2 and listed in Table S1. Generalized linear mixed model analysis of response accuracies (see *2.4. Behavioral analyses*) yielded a significant effect of condition ($\chi^2(3) = 216.0$, $p < .001$) as well as a significant age × condition interaction ($\chi^2$ (3) = 22.0, $p < .001$) with no effect of age ($\chi^2$ (1) = 0.223, $p = .637$). Examination of pair-wise contrasts was anchored to the intercept being young adult response accuracy for the baseline AX condition. These pair-wise comparisons showed that the condition main effect was characterized by significant negative effects of trial type for AY, BX and BY compared with the baseline AX condition (AY: b(SEM) = −3.08 (0.255), $p < .001$; BX: b(SEM) = −2.67 (0.267), $p < .001$; BY: b(SEM) = −3.93 (0.275), $p < .001$). Critically, the age × condition interaction was qualified by negative effects of age for BX (b(SEM) = −0.878 (0.378), $p = .02$) and BY (b(SEM) = −0.842 (0.40), $p = .035$) but not AY (b(SEM) = 0.339 (0.381), $p = .373$) relative to young AX accuracies.

We note that variances were unequal between age groups for mean response accuracy in the BY condition ($F(1, 40) = 4.21$, $p = .047$) reflecting greater individual variability in older adults for this condition. However, age differences in variances were not significant in other conditions (AX: $F(1, 40) = 0.114$, $p = .738$; AY: $F(1, 40) = 0.108$, $p = .774$; BX: $F(1, 40) = 1.39$, $p = .245$). Overall, whereas A-cue accuracies were comparable across age, older adults showed lower accuracy under B-cue than A-cue contextual processing.

### 3.2. Reaction time slowing from correct AX to AY and to B-cue trials greater in old than young

Linear mixed model analysis of correct trial reaction times yielded significant main effects of condition ($F(3, 112.6) = 184.18$, $p < .001$), age ($F(1, 40.6) = 17.45$, $p < .001$), and a significant age × condition interaction ($F(3, 112.6) = 4.56$, $p = .004$). Pair-wise comparisons revealed significantly slower reactions for AY, BX and BY compared with baseline AX condition (AY: b(SEM) = 265.2 (24.0), $p < .001$; BX: b(SEM) = 301.0 (24.0), $p < .001$; BY: b(SEM) = 340.9 (26.1), $p < .001$), and for older compared with young adults (b(SEM) = 107.5 (44.0), $p = .018$). The

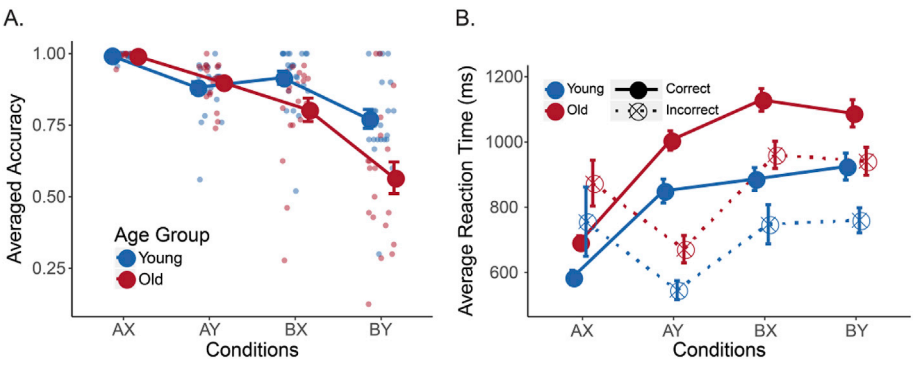


**Fig. 2. Young and older behavioral responses in the XDPX task.** (A) Mean group (bigger opaque circles) and individual (smaller transparent circles) accuracies calculated as the number of correct response trials/number of responded trials across condition trial types. (B) Mean group reaction times calculated based on participant reaction time means across condition trial types. Correct response trial reaction times are shown in solid lines with filled circles and incorrect response reaction times in dotted lines with empty x-circles. Error bars indicate S.E.M. See also Table S1.

age × condition interaction was characterized by slower reaction times in BX relative to the AX condition in older compared to younger adults (AY: b(SEM) = 46.4 (35.8), p < .20; BX: b(SEM) = 132.5 (36.1), p < .001; BY: b(SEM) = 48.4 (40.6), p = .25).

### 3.3. Reaction times slower for incorrect B-cue than AY trails for both young and old

Analysis of incorrect trial reaction times yielded significant main effects of condition (F(3, 362.8) = 24.7, p < .001) and age (F(1, 42.2) = 20.7, p < .001), but no significant age × condition interaction (F(3, 362.8) = 0.475, p = .70). Pair-wise comparisons revealed that older adults generally showed significant longer reaction times than younger adults (b(SEM) = 185.8 (79.6), p = .020), as expected. Also, the main effect of condition stemmed from significantly faster reaction times for incorrect AY trials (b(SEM) = −244.8 (58.8), p < .001) relative to the AX condition, but not for incorrect B-cue related trials (BX: b(SEM) = −55.1 (59.6), p = .356; BY: b(SEM) = −28.3 (60.7), p = .642).

Overall, older adults evinced generally longer reaction times compared to young adults particularly when correctly responding to BX conditions. Critically, whereas incorrectly responded AY trials might be attributed to premature faster responses, incorrect BX and BY responses were as slow as AX responses and thus might reflect additional difficulties in cognitive processing apart from failure of motor inhibition.

### 3.4. Proactive cortical responses to contextual cues in young but not older adults

In separate group analyses, whole-brain contrasts of contextual cue processing yielded higher functional brain responses to B-cue than A-cue contexts for both young and older adults with no regions showing the reverse cue effect (Fig. 3 and Table S2; see Fig. S1 for cortical surface view of [B-cue – A-cue]$_{Young}$; see Fig. S2A and Fig. S2B for separate age group whole brain neural responses for A- and B-cue relative to baseline, respectively).

However, whereas both young and older adults showed significant cue effects (higher B-cue than A-cue responses) in bilateral putamen, extensive cortical cue effects in bilateral frontal, parietal, temporal, occipital, and insula areas were observed in young adults only (Fig. 3A). Directly comparing age differences in whole brain neural activity revealed significantly greater dissociation of B-cue vs. A-cue responses in younger than older adults in midbrain areas (around the superior colliculi and periaqueductal gray) extending into the parahippocampal gyri (Fig. 3C and Table 1). No brain areas showed cue effects that were greater in older than younger adults.

### 3.5. Reactive cortical modulation during AY probe processing greater in old than young

A broad extent of brain areas showed higher neural responses

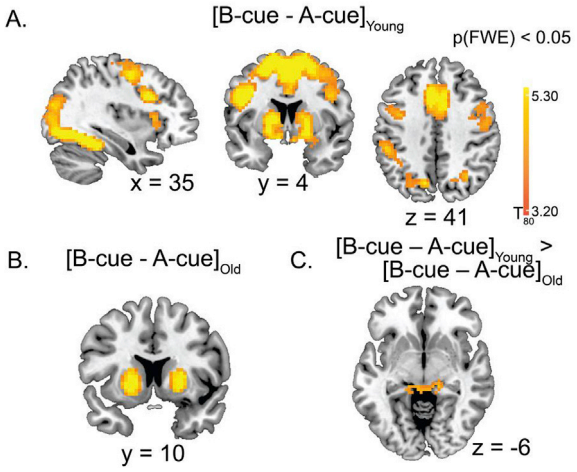


**Fig. 3. Whole-brain results of contextual cue processing.** Statistical map overlays on brain slices showing age differences in neural responses during contextual cue processing (B-cue - A-cue). (A) B-cue effects in young adults were observed in bilateral mediolateral frontoparietal, visual, and subcortical areas as well as insula. (B) B-cue effects in older adults were observed in subcortical areas only. (C) Brain areas showing significantly higher B-cue relative to A-cue response contrast in younger than older adults were observed in midbrain areas extending into bilateral parahippocampal gyri (see also Table 1 and Table S2). Significance thresholds for whole-brain contrasts were set at p < 0.001, cluster-size at least 48 voxels, which fulfilled whole-brain p(FWE) < 0.05.

associated with correct inhibition of stimulus-response prepotency during AY compared to AX probes across both young and older adults including bilateral angular gyrus, supplementary motor, temporal, parietal, precuneus, inferior and middle frontal, occipital, insula, and subcortical areas (Table S3, Fig. S2C). Direct whole-brain contrasts of age differences revealed that older adults had higher neural recruitment for AY relative to AX probe conditions compared to younger adults in exclusively left hemisphere cortical regions, including angular gyrus, inferior and middle frontal, medial frontal, and middle temporal regions (Fig. 4A, Table 2; see Fig. S3 for brain surface view of Fig. 4A). No brain areas showed higher contrast responses in younger compared to older adults for the AY relative to AX condition.

We then evaluated the associations between neural responses for AY probes in functional ROIs defined from the above direct age difference whole-brain contrast (Table 2; see *2.7. Functional regions-of-interest (ROI) analysis*) with behavioral performances. There were no significant associations between AY accuracy and AY condition neural responses in these ROIs. Nevertheless, lower AY neural responses significantly correlated with longer AY probe correct reaction times in older but not younger adults in the left medial superior frontal gyrus (L MedSFG; MNI: 9, 45, 42; old: r = -.56, p(FDR) = .031; young: r = -.08, p(FDR) = .991) (Fig. 4B).

However, regression analyses with age and AY brain responses

**Table 1**
List of peak voxel locations and statistics for brain areas showing age differences (Young > Old) in higher B-cue than A-cue neural responses at $p < 0.001$, cluster-size of at least 48 voxels (whole-brain p(FWE) < 0.05). See Table S2 for separate group results.

| Regions | L/R | BA | k | Cluster-wise p (unc.) | T | x | y | z |
|---|---|---|---|---|---|---|---|---|
| Midbrain | L | – | 125 | <0.001 | 5.38 | −6 | −33 | −9 |
| Midbrain | R | – | – | – | 4.46 | 12 | −27 | −9 |
| Parahippocampal Gyrus | R | 27 | – | – | 4.44 | 15 | −30 | −3 |
| Parahippocampal Gyrus | L | 27 | – | – | 3.96 | −15 | −30 | −6 |

L: Left hemisphere, R: Right hemisphere, BA: Brodmann's Area, k: cluster size; - in cluster size field denote contiguous brain areas.

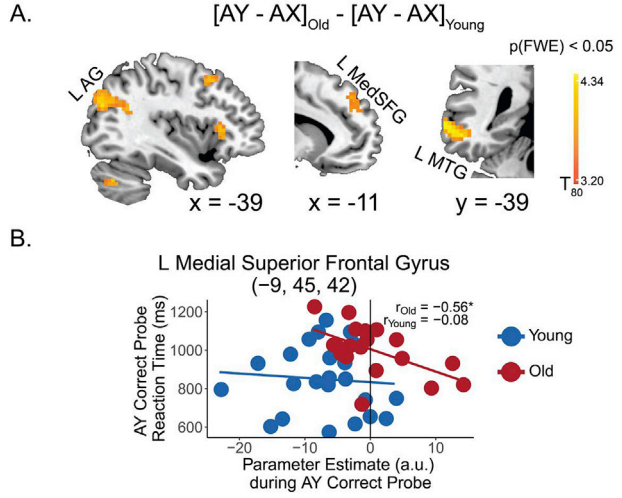


**Fig. 4. Age differences in neural responses and behavioral associations during prepotency inhibition (AY - AX).** (A) Whole-brain contrast showing areas with higher neural activity during correct AY probe responses relative to the AX condition in older than younger adults (see also Table 2, Table S3 and Fig. S3). Age effects were observed only in left hemisphere, including medial prefrontal cortex (L MedSFG), angular gyrus (L AG), angular gyrus, left middle and inferior frontal gyrus, and left middle temporal gyrus (L MTG). Significance threshold for whole-brain contrast was set at $p < 0.001$, with cluster size >48 voxels, fulfilling whole-brain cluster-wise FWE adjusted $p < 0.05$. (B) Scatterplot of AY correct response reaction times by neural response parameter estimates during correct AY response trials in ROI from the whole-brain contrast in (A). Older but not younger adults showed significant negative correlations in left medial superior frontal gyrus, although linear regression showed no significant age interaction. Pearson correlation coefficients were corrected for multiple comparisons using FDR.

**Table 2**
List of peak voxel locations and statistics for brain areas showing age differences (Old > Young) in higher AY than AX probe neural responses (correct trials) at $p < 0.001$, cluster-size of at least 48 voxels (whole-brain p(FWE) < 0.05). See Table S3 for separate group results.

| Regions | L/R | BA | k | Cluster-wise p (unc.) | T | x | y | z |
|---|---|---|---|---|---|---|---|---|
| Middle Temporal Gyrus | L | 21 | 119 | <0.001 | 4.32 | −63 | −39 | −6 |
| Middle Frontal Gyrus | L | 8 | 73 | 0.003 | 4.26 | −30 | 18 | 45 |
| Inferior Frontal Gyrus *tri.* | L | 45 | 57 | 0.008 | 4.16 | −42 | 24 | 3 |
| Medial Superior Frontal Gyrus | L | 8 | 48 | 0.013 | 3.64 | −9 | 45 | 42 |
| Angular Gyrus | L | 19 | 214 | <0.001 | 4.05 | −39 | −75 | 27 |

L: Left hemisphere, R: Right hemisphere, BA: Brodmann's Area, k: cluster size; - in cluster size field denote contiguous brain areas.

predicting RT yielded no significant Age × AY brain response interaction effects in L medSFG. Thus, while older individuals with greater neural resource engagement in left medial superior frontal gyrus showed significantly greater facilitation of prepotent response inhibition for the AY condition, the association of neural processing with AY performance did not differ significantly across age groups. We also evaluated whole-brain contrasts of AY probe neural responses based on accuracy (see Supplemental Data). However, because neural responses in these brain areas did not necessarily distinguish between AY and AX probe conditions, they are not of focus in this current study.

### 3.6. DMN activation higher to correct than incorrect B-cue probe trials in old but not young

Distinct from AY probe responses, whole-brain contrast of age differences in correct trial probe responses under B-cue contexts (BX and BY jointly) relative to AX revealed significantly higher neural responses in older compared to younger adults across several brain areas part of the DMN and medial temporal lobe (MTL) (Fig. 5A, Table 3; see Fig. S2D and Table S4 for separate age group results; for surface view of Fig. 5A, see Fig. S4).

These included posterior cingulate cortex, bilateral precuneus, temporoparietal (spanning angular gyri and posterior superior temporal gyrus), medial frontal, lateral temporal, parahippocampal, and hippocampal areas. Other brain areas observed included bilateral superior frontal, orbitofrontal, and left fusiform, lingual, and occipital areas. No regions showed higher responses to B-cue related probes in younger than older adults. Note that separately contrasting BX or BY relative to AX probes also revealed older adults had higher neural responses than younger adults in similar areas (Figs. S5A and B; see Table S5 and Figs. S2E and F for separate age group results). In addition, contrasting BY relative to BX probes evinced higher neural activity in older than younger adults as well in the right fusiform gyrus, hippocampus, parahippocampal gyrus, middle and inferior temporal areas, and left amygdala and temporal areas (Fig. S5C; see Table S5 and Fig. S2G for separate age group results).

Critically, we evaluated whether neural responses in the above DMN and MTL regions were higher or lower than rest baseline, and how the neural responses were associated with accuracy of BX and BY probe responses in young and older adults. For each DMN and MTL ROI defined using the contrast peaks locations in Table 3 (see *2.7. Functional regions-of-interest (ROI) analysis*), we applied a linear mixed model regression on probe neural response estimates with trial types (AX, BX, incorrect BX, BY, incorrect BY) and age group (young and old) as fixed effects and subjects as a random effect (young adult AX response was the intercept). We then identified key ROIs in which (1) there were significant age differences in the responses to correct but not incorrect BX and BY conditions based on the regression coefficients from the above model, (2) young adults showed significantly suppressed neural responses estimates (lower than rest baseline) to correct BX and BY conditions, and (3) older adults showed significantly active neural responses (higher than rest baseline) to BX or BY conditions that were correctly responded to.

Three DMN ROIs (Fig. 5B) fulfilled the above three criteria including the left (L MedSFG; MNI: 12, 66, 18; BX correct: $b_{Age}(SEM) = 19.75\ (6.85)$, $p(FDR) = .014$, Hedges'g = 1.38; $t_{young}(22) = -4.67$, $p(FDR) < 0.001$,

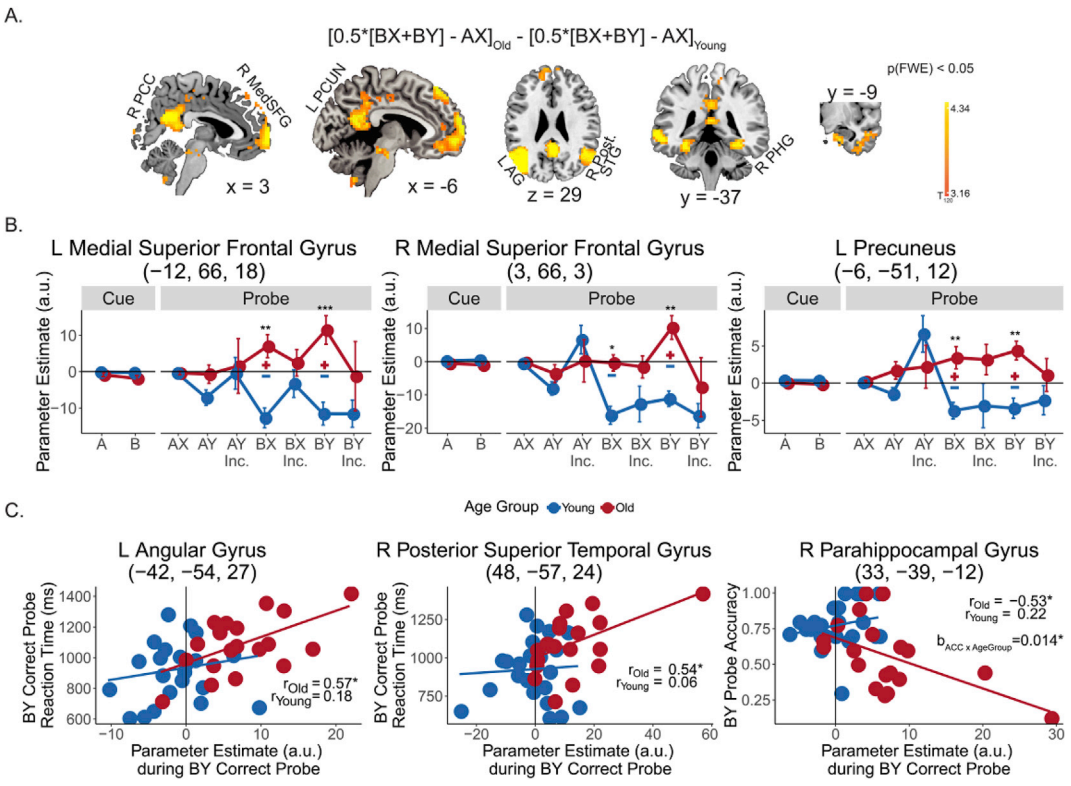


**Fig. 5. Age differences in neural responses during non-linear contextual processing ([BX + BY]*0.5 - AX) and behavioral associations.** (A) Brain areas showing higher neural activity during correct B-cue probe responses relative to the AX condition in older than younger adults. These areas encompassed DMN regions including medial superior frontal gyrus (MedSFG), angular gyrus (AG), posterior superior temporal gyrus (Post. STG), precuneus (PCUN), posterior cingulate gyrus (PCC), lateral temporal area, parahippocampal gyrus (PHG), and hippocampus, amongst others (see Table 3 and Table S4). Significance threshold for whole-brain contrast was set at $p < 0.001$, with cluster size >48 voxels, fulfilling whole-brain cluster-wise FWE adjusted $p < 0.05$. (B) Neural response parameter estimates across cue and probe trial types in DMN ROIs from (A) that showed significant age differences in correct but not incorrect BX and BY probe response trials as well as with older adults showing positive and young adults showing negative probe neural responses relative to baseline. Error bars show S.E.M. Asterisks denote significant trial type neural response age differences at $p < 0.05$ (*), $p < 0.01$ (**), and $p < 0.001$ (***). Red "+" signs denote significant neural activation response relative to baseline (parameter estimate > 0) in older adults, p(FDR) < 0.05. Blue "-" sign denote significant neural suppression response relative to baseline (parameter estimate < 0) in young adults, p(FDR) < 0.05. (C) Scatterplots of neural activity during correct BY response trials by BY correct response reaction time and BY accuracy for DMN ROIs from (A). Associations between neural responses and behavior were significant in older but not younger adults (see main text results; also Fig. S6). * denote significant association at p(FDR) < 0.05.

Cohen's d = -.97; $t_{old}(18) = 2.22$, p(FDR) = .02, Cohen's d =.50; BY correct: $b_{Age}(SEM) = 23.06$ (6.85), p(FDR) = .001, Hedges'g = 1.35; $t_{young}(22) = -3.70$, p(FDR) = .001, Cohen's d = -.77; $t_{old}(18) = 2.93$, p(FDR) = .006, Cohen's d = .67) and right medial superior frontal gyrus (R MedSFG; MNI: 3, 66, 3; BX correct: $b_{Age}(SEM) = 15.45$ (6.51), p(FDR) = .028, Hedges'g = 1.23; $t_{young}(22) = -5.98$, p(FDR) < 0.001, Cohen's d = -1.25; BY correct: $b_{Age}(SEM) = 21.16$ (6.51), p(FDR) = .002, Hedges'g = 1.53; $t_{young}(22) = -4.89$, p(FDR) < 0.001, Cohen's d = −1.02; $t_{old}(18) = 2.89$, p(FDR) = .006, Cohen's d = .66), and left precuneus (L PCUN; MNI: 6, −51, 12; BX correct: $b_{Age}(SEM) = 7.00$ (2.64), p(FDR) = .015, Hedges'g = 1.143; $t_{young}(22) = -3.36$, p(FDR) = .003, Cohen's d = -.70; $t_{old}(18) = 2.30$, p(FDR) = .017, Cohen's d = .53; BY correct: $b_{Age}$(-SEM) = 7.62 (2.64), p(FDR) = .004, Hedges'g = 1.21; $t_{young}(22) = -2.52$, p(FDR) = .013, Cohen's d = -.53; $t_{old}(18) = 3.44$, p(FDR) = .003, Cohen's d = .79). Overall in these ROIs where neural responses were differentially associated with accurate behavior in young and older adults, correct BX and BY responses were associated with lower than baseline neural responses in younger adults but higher than baseline responses in older adults. Similarly, in all the other ROIs (Fig. S6), neural responses were generally higher for correct than incorrect BY probe trials in older adults, with B-cue probe responses in older adults either significantly higher or no different than rest baseline and B-cue probe responses in younger adults either significantly lower or no different than rest baseline.

Finally, we evaluated the associations between B-cue related probe neural responses in the ROIs from Table 3 with individual behavioral performance. Higher correct BY probe neural responses in bilateral temporoparietal regions correlated with longer correct BY probe reaction times in older but not young adults (L Angular Gyrus; MNI: 42, −54, 27; old, r = .57, p(FDR) = .033; young, r = .18, p(FDR) = .486; R Post. Superior Temporal Gyrus; MNI: 48, −57, 24; old, r = .54, p(FDR) = .043; young, r = .06, p(FDR) = .80) (Fig. 5C). Higher correct BY probe neural responses in right parahippocampal gyrus correlated with lower accuracy during BY probe in older but not young adults (R Parahippocampal Gyrus; MNI: 33, −39, −12; old: r = .53, p(FDR) = .044; young: r = .22, p(FDR) = .396). Moreover, regression analyses with age and correct BY probe neural responses predicting accuracy revealed that the Age × correct BY probe neural response interaction was significant in R PHG ($b_{Age*BY}(SEM) = -.0138$ (0.010), p(FDR) = .037). Evaluations of whole-brain contrasts of B-cue probe neural responses based on accuracy are described in Supplemental Data. However, neural responses in these brain areas did not necessarily distinguish between A- and B-cue probe conditions unlike the above ROIs showing accuracy-based B-cue probe response differences relative to AX responses, and as such they are not of focus in this current study.

### *3.7. Young-like proactive neural responses associated with better performance and less DMN involvement during B-cue probe processing*

Additional ROI correlation analyses were conducted to examine the extent to which older and younger individuals that engaged higher cue-

**Table 3**
List of peak voxel locations and statistics for brain areas showing age differences (Old > Young) in higher B-cue probe responses than AX probe neural responses ((BX + BY)*0.5 > AX; correct trials) at $p < 0.001$, cluster-size of at least 48 voxels (whole-brain p(FWE) < 0.05). See Table S4 for separate group results.

| Regions | L/R | BA | k | Cluster-wise p (unc.) | T | x | y | z |
|---|---|---|---|---|---|---|---|---|
| Middle Occipital Gyrus | L | 39 | 551 | <0.001 | 6.56 | −42 | −78 | 33 |
| Angular Gyrus[a] | L | 39 | – | – | 5.64 | −42 | −54 | 27 |
| Angular Gyrus[a] | R | 39 | 290 | <0.001 | 6.12 | 45 | −72 | 42 |
| Post. Superior Temporal Gyrus[a] | R | 39 | – | – | 4.80 | 48 | −57 | 24 |
| Precentral Gyrus | R | 4 | 120 | 0.001 | 4.04 | 30 | −24 | 60 |
| Orbitofrontal Cortex | R | 47 | 173 | <0.001 | 5.78 | 27 | 33 | −12 |
| Orbitofrontal Cortex | L | 47 | 1458 | <0.001 | 5.83 | −27 | 33 | −15 |
| Superior Frontal Gyrus | L | 9 | – | – | 5.32 | −24 | 42 | 45 |
| Superior Frontal Gyrus | R | 9 | – | – | 4.32 | 24 | 42 | 48 |
| Medial Superior Frontal Gyrus[a] | L | 10 | – | – | 5.20 | −12 | 66 | 18 |
| Medial Superior Frontal Gyrus[a] | R | 10 | – | – | 4.87 | 3 | 66 | 3 |
| Posterior Cingulate Gyrus[a] | – | 23 | 619 | <0.001 | 5.16 | 0 | −48 | 27 |
| Precuneus[a] | L | 30 | – | – | 4.38 | −6 | −51 | 12 |
| Precuneus[a] | R | 29 | – | – | 5.11 | 9 | −48 | 12 |
| Middle Temporal Gyrus | L | 21 | 285 | <0.001 | 5.62 | −66 | −36 | 0 |
| Inferior Temporal Gyrus | R | 20 | 265 | <0.001 | 4.78 | 42 | −6 | −39 |
| Middle Temporal Gyrus | R | 21 | – | – | 4.47 | 63 | 0 | −24 |
| Temporal Pole | R | 38 | – | – | 4.11 | 48 | 12 | −36 |
| Fusiform Gyrus | L | 37 | 317 | <0.001 | 4.94 | −33 | −39 | −15 |
| Parahippocampal Gyrus[a] | L | 36 | – | – | 4.70 | −24 | −36 | −9 |
| Lingual Gyrus | L | 19 | – | – | 3.95 | −27 | −63 | −6 |
| Fusiform Gyrus | R | 37 | 305 | <0.001 | 4.95 | 33 | −33 | −18 |
| Parahippocampal Gyrus[a] | R | 37 | – | – | 4.63 | 33 | −39 | −12 |
| Hippocampus[a] | R | 36 | – | – | 4.21 | 21 | −9 | −27 |
| Hippocampus[a] | L | 35 | – | – | 3.72 | −21 | −15 | −21 |
| Midbrain | L | – | – | – | 4.35 | −6 | −27 | −15 |
| Midbrain | R | – | – | – | 3.91 | 6 | −33 | −15 |

[a] DMN and medial temporal regions of interest. L: Left hemisphere, R: Right hemisphere, BA: Brodmann's Area, k: cluster size, Post.: Posterior; - in cluster size field denote contiguous brain areas.

related neural responses would show better behavioral performances and also engage lower probe-related processing (i.e. more proactive processing). In general, across the ROIs showing higher B- than A-cue responses in young adults (Table S2), higher B-cue neural responses in young adults correlated with higher BX and BY accuracy and faster BX reaction times (Table S6). Higher B-cue neural responses in young adults also positively correlated with correct BX neural responses in the left hippocampus and with correct BY neural responses across bilateral medial temporal, precuneus, medial superior frontal, left angular areas (Table S7). In other words, higher contextual B-cue processing in young adults was associated with better B-cue probe performances, as well as lessened task-induced deactivation during correct B-cue probe processing in the DMN and MTL ROIs. For older adults, in the same cue-related ROIs defined from young adult brain responses, higher occipital B-cue neural responses in older adults correlated with faster older adult BY probe response time. Higher B-cue neural responses in bilateral occipital area and precuneus, and left supplementary motor and parietal areas in older adults also correlated with higher BY accuracy (Table S6). Critically, higher older adult B-cue neural responses collectively showed negative correlations with neural responses during B-cue probes across several DMN and MTL ROIs. Higher B-cue neural responses in right middle occipital, left fusiform, insula and midbrain ROIs correlated with lower correct BX neural responses in left medial frontal, and angular areas, and right parahippocampal gyrus. Finally, higher B-cue neural responses in bilateral fusiform, middle and superior occipital areas, insula, and precuneus, and left supplementary motor, putamen, and superior parietal ROIs correlated with lower correct BY probe neural responses across bilateral medial frontal, temporoparietal, precuneus, posterior cingulate, and medial temporal areas (Table S7).

## 4. Discussion

We report a critical involvement of DMN regions in normal human older adults in successful integration of cue-probe information when processing non-linear contextual problems. In the XOR problem presented in our XDPX task, young adults engaged greater lateral frontoparietal responses to distinguish between contextual cues compared to older adults reflecting proactive cue processing in the former with reduced need to engage non-linear processing during probes, consistent with previous studies (Braver et al., 2001; Paxton et al., 2008; Rush et al., 2006). By contrast, older adults showed less distinctive neural processing between cues but evinced enhanced responses to probes, consistent with a more reactive strategy also as suggested in previous studies. Importantly, correct performance for older adults in probe conditions driving the non-linear cue-probe response mappings (BX, BY conditions) was associated with higher responses in DMN (and MTL) regions compared to incorrect performance. Moreover, brain responses in DMN regions for correct performance in older adults were characterized by enhanced *activity* relative to baseline fixation responses, in contrast to the suppression of DMN regions activity during task processing seen in the young adult group and typically reported in other studies (Anticevic et al., 2012; Fox et al., 2005; Shulman et al., 1997). Finally, older individuals with higher cue-related neural processing showed better performances and lower engagement of the DMN regions during BY probes. We suggest that our findings reflect age-related differences in neurocognitive resource allocation such that the DMN is engaged in normal older adults for retrospective retrieval and integration of cue-probe contextual associations that are complex and for which processing in other brain areas are insufficient to resolve.

Consistent with previous studies, we found that frontal and parietal regions were engaged in younger adults to proactively process contextual cues ahead of probes, with neural responses that distinguished B-cues from A-cues. These brain regions are centrally implicated in executive operations such as attentional and goal-directed control (Banich, 2009; Gilbert and Burgess, 2008; Miyake et al., 2000; Niendam et al., 2012; Egner and Hirsch, 2005; Hughes et al., 2014). We speculate that such proactive processing of contextual cues involves neural computations to predictively filter and select from competing rule sets as soon as information to do so is available. In so doing, the XOR problem can be reduced into a set of linear problems for the given contextual cue. For example, in

the XDPX task, once a B-cue is seen, the participant can focus on a simple linear rule to make a non-target response if an X-probe is next seen, and a target response otherwise. Thus, a proactive strategy that actively and predictively selects subsets of potential future responses might reflect one type of neural network solution to non-linear problems that predominantly relies on brain regions involved in attention and task switching processes. Interestingly, young adults also engaged significantly higher midbrain activity than older adults during B-cue processing in our study. This result is consistent with a recent similar finding using the AX-CPT paradigm (Mäki-Marttunen et al., 2019) and may reflect involvement of midbrain nuclei in context updating as well.

Such proactive computation, however, involves sustained vigilant neural monitoring to identify and process contextual affordances that, although facilitating less subsequent neural processing for behavioral contingencies, require neural resource capacities at the outset for which older adults may not readily engage (Paxton et al., 2008; Campbell et al., 2012; Fisk and Sharp, 2004; West et al., 2002; Goh, 2011; Mayda et al., 2011). Indeed, a more reactive strategy geared to only engage excess neural processing to probes when required would be more economical in the long run if complex problems were less frequent. As such, one reason why older adults engage reactive processing might be due to age-related alterations in neural resource allocation perhaps because of biological changes affecting neural processing efficacy (Bäckman et al., 2006; Li et al., 2001). Alternatively, older adults might be used to less complex daily experiences compared to younger adults (Anstey and Smith, 1999; Anguera et al., 2013; Gates and Valenzuela, 2010; Salthouse, 2006) or undergo motivational changes related to differences in life goals (Carstensen et al., 1999). In either case, recruitment of DMN regions *activity* to aid accurate behavioral decisions during complex contextual processing in older adults reflects yet another neural network solution for non-linear rule-response mappings. These findings are consistent with recent proposals regarding the role of the DMN in older adult control processing (Spreng and Turner, 2019).

It is possible that some of the brain regions identified as part of the DMN using the contrast of B-cue probe > AX responses in older vs. younger adults might be involved in non-DMN-related processing instead. For instance, angular gyri activity has also been reported to be involved in several distinct functions (Seghier, 2013). However, in our study, only ROIs in which task-related responses in young adults were significantly lower than resting fixation baseline were considered as part of the DMN. This is in line with the canonical definition of the DMN has brain regions responding with lower than rest baseline activity during task conditions (Andrews-Hanna et al., 2014; Buckner et al., 2008; Dixon et al., 2014; Orr and Banich, 2014; Raichle, 2015). Importantly, neural responses for correct but not incorrect B-cue probe responses in these brain areas showed significant age differences, with equal or higher than baseline in older adults but significantly lower than baseline in younger adults.

We note that there were minimal age differences in young and older ability to inhibit the prepotent target response to AX probes during AY trials in terms of behavioral accuracy. Mixed data have been reported in the literature on age differences in inhibitory control. Some studies suggest age-related declines in cognitive inhibition underlying older adults being more influenced by irrelevant information than younger adults (Hasher and Zacks, 1988; Nielson et al., 2002; Bedard et al., 2002), whereas others find no significant age differences in the ability to suppress dominant or automatic responses (Rush et al., 2006; Williams et al., 1999). We suggest that such mixed findings on age differences in inhibitory control stem from differences in experimental operationalization of inhibition across studies. In this present study, inhibition was assessed by the ability to suppress behavioral responses to target stimuli that have prepotent mappings due to frequent encounters and are thus more automatized. Our findings suggest that this ability to contingently suppress simple responses automatized by frequent exposure might be a relatively preserved neural function between young and older adults with minimal age differences in performance accuracy, at least for linear problems involving visual symbols and one-finger button presses.

Nevertheless, despite age-comparable behavioral inhibition of prepotent responses, older adult RTs were generally slower and they also engaged additional neural responses relative to younger adults in medial and lateral frontal, insula, angular gyrus, and temporal areas, exclusively in the left hemisphere, during correct AY response trials. While such age-related increase in task-related neural activity is in line with compensatory engagement in aging brain function (Cabeza et al., 2002; Reuter--Lorenz and Cappell, 2008; Goh and Park, 2009), we highlight that compensatory neural extra-recruitment in older adults is typically observed in lateral frontoparietal areas. By contrast, the medial frontal region and angular gyri are part of the DMN. Moreover, older individuals with higher neural activity in the medial frontal regions enhanced the speed of their accurate AY non-target responses. These findings are difficult to reconcile with putative additional compensatory processing, in which higher neural activity should be associated with longer reactions times. We suggest that additional involvement of DMN processing might reflect more veridical retrospective processing of cue-probe response mappings under a reactive approach in older adults that contributes to faster inhibition of target response prepotency for AY trials. Overall, it is noted that different DMN networks are functionally distinct (Raichle, 2015; Vincent et al., 2006; Gusnard et al., 2001; Andrews-Hanna et al., 2010) and further studies parsing different types of retrospective retrieval are necessary to specify the unique computations in different DMN areas in relation to cognitive control and age-related differences in strategy.

It is interesting to note that older individuals who evinced more young-like engagement with higher responses to contextual cues and less DMN (and MTL) engagement during related probes showed better behavioral performance. We suggest that this finding reflects individual differences in the neurocomputational resources available in older adult brain function. Specifically, older adults who are able to recruit sufficient neural resources to engage in more proactive cue-probe response mapping selection would do so. By contrast, older adults whose resource cap prevents the sustained engagement of proactive strategies then rely on reactive strategies to meet task performance goals, albeit still with performance costs under more complex situations. In this light, we suggest that the frequent observation of less task-related DMN suppression in older adults (Andrews-Hanna et al., 2007; Damoiseaux et al., 2007; Grady et al., 2009; Park et al., 2010; Persson et al., 2007; Sambataro et al., 2010; Spreng et al., 2016; Turner and Spreng, 2015) might reflect operation of task-relevant rather than task-irrelevant introspective processes during experimental rest periods. Future studies are necessary to validate these above notions, in particular why proactive processing might be preferred under resource-rich conditions such as in younger adults but reactive processing is preferred under resource-poor conditions such as in older adults.

We note that the experimental task was of marked difficulty for older than younger adults. In the course of the training and practice phases of the experiment as well, experimenters reflected that young adults were able to learn the XOR rules of the XDPX task with relative efficacy. However, many older participants grasped the semantic rules of the task only after extended instruction and guidance, with more older than younger adults excluded due to indications of inability to comprehend the task rules. In addition, although all participants in the analyzed sample passed the minimal training criteria indicating understanding of the task rules, older adults nonetheless still showed about chance level accuracy performance in BY condition as a group. One related concern might be the validity of estimates of BY-related neural responses given the chance performance and low trial numbers available. Our results from ROI analysis showed clear reliable dissociations between correct and incorrect BY trial responses in target brain areas in older adults suggesting that effect sizes afforded sufficient power for detecting meaningful neural responses. Also, it is possible that there is a selection bias in our sample of higher performing older adults meeting our XDPX behavioral criteria (see *2.2. XDPX stimuli and procedures*). We note that

such a sample bias stemming from our behavioral exclusion criteria would in fact work against finding effects in this study. Specifically, high performing older adults should behaviorally be more comparable to young adults and should engage brain activity less differently than younger adults. Indeed, our results demonstrate that older adults who had better XDPX performance had more young-like proactive neural responses. Despite this, we still found that this group of relatively high performing older adults engaged higher neural activity for correct than incorrect responses in default mode network and medial temporal areas, which was not seen in the young adult sample. As such, we suggest that in future studies targeting a less biased sample of older adults where poorer performing older adults are included, age differences in neural responses during XDPX correct performance should be even more accentuated. Overall, we highlight that our older adult sample is likely a select group relatively high functioning individuals displaying adequate performance in our complex task, albeit individual differences are still evident with increasing difficulty of the computational demands in the task. Indeed, there was significantly greater individual variability in BY accuracies for older than younger adults. Further study with large older adult samples to evaluate individual differences in ability to grasp and apply complex rules are critical to understanding neural architectures underlying more optimal non-linear information processing.

Finally, we point out that the engagement of proactive contextual processing in lateral frontoparietal areas or reactive processing in DMN to process non-linear cue-probe mappings in the XDPX task is akin to the role of hidden layers in solving XOR problems in neural network modeling (Rumelhart et al., 1986). Hidden layers are hierarchically in the center of neural networks that are enabled to solve XOR problems, relative to the input and output layers. It is tempting here then to consider the analogy that one of the deepest of XOR problems that the brain neural network has to solve is the consistency of self-related input-output mappings across different contingent experiences. While speculative, we propose that this might be a framework for understanding the involvement of the DMN in older adults when using a reactive strategy for non-linear problems, in comparison to proactive strategies that can reduce non-linear problems to simple linear solutions. From this, greater expression of or reliance on this self-processing network when generating behavioral response to contextual contingencies might be then be construed as a key hallmark of the human cognitive brain in advanced age.

## Author contributions

Conceptualization, C.C.C., Y.Z.T. and J.O.S.G.; Methodology, C.C.C., J.O.S.G. and Y.Z.T.; Software, C.C.C., Y.S.S. and J.O.S.G.; Formal Analysis, C.C.C.; Investigation, C.C.C.; Writing – Original Draft, C.C.C. and J.O.S.G.; Writing – Review & Editing, J.O.S.G. and Y.Y.S.; Visualization, C.C.C.; Funding Acquisition, J.O.S.G.

## Declaration of interests

The authors declare no competing interests.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuroimage.2019.116012.

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