

# Distinct profiles of stimulus specific cortical activity for ignoring distraction during working memory encoding and maintenance, and associations with performance

**Charlotte Ashton**

University of York

**André Gouws**

York Neuroimaging Centre

**Marcus Glennon**

University of York

**THEODORE ZANTO**

UCSF

**Steve Tipper**

University of York

**Fiona McNab** (✉ [fiona.mcnab@york.ac.uk](mailto:fiona.mcnab@york.ac.uk))

University of York

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## Article

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# Abstract

Our ability to hold information in mind for a short time (working memory) is separately predicted by our ability to ignore two types of distraction: distraction that occurs while we put information into working memory (encoding) and distraction that occurs while we maintain already encoded information within working memory. This suggests that ignoring these different types of distraction involves distinct mechanisms which separately limit performance. Here we used fMRI to measure category-sensitive cortical activity and probe these mechanisms. The results reveal specific neural mechanisms by which relevant information is remembered and irrelevant information is ignored, which contribute to intra-individual differences in WM performance.

## Introduction

Our ability to effectively exclude distraction and selectively attend to relevant stimuli has been identified as a basis for Working Memory Capacity (WMC) limitations in younger adults, older adults and in patients<sup>1,2,3,4</sup>.

Using functional magnetic resonance imaging (fMRI) with sequential presentation of single stimuli or superimposed images, there have been reports of “enhancement” of activity associated with stimuli that viewers are instructed to remember, and “suppression” of activity associated with stimuli that are to be ignored, relative to a stimulus-matched passive view baseline<sup>5,6,7</sup>. A reduction in this suppression may contribute to impaired Working Memory (WM) performance associated with healthy ageing<sup>8,9,10</sup>.

However, separate behavioral work has identified two potential bases for our limited WMC: a person’s ability to ignore irrelevant stimuli that appear with the stimuli that should be remembered (during encoding; “Encoding Distraction”, ED) and their ability to ignore irrelevant stimuli during the WM delay period, when relevant stimuli are held in mind but no longer physically present (“Delay Distraction”, DD)<sup>11</sup>. Our behavioral findings indicate that our ability to ignore ED and DD uniquely predict WMC<sup>11</sup> and are differentially affected by ageing<sup>12</sup>, suggesting separate mechanisms. The nature of these mechanisms, is not yet known.

Here we used face and scene stimuli to examine cortical activity associated with remembering task-relevant stimuli and ignoring task-irrelevant stimuli during a WM task with No overt Distraction (ND), with ED, or with DD (Figure 1). For this remember/ignore task, we refer to stimuli to be remembered as “primary stimuli” and the stimuli to be ignored as “secondary stimuli”. When faces were the primary stimuli, scenes were the “secondary stimuli”, and vice versa. We compared each of these conditions to a separate “passive view” task, which involved identical presentation of primary and secondary stimuli, but for this task none of the stimuli were to be remembered.

With a separate ANOVA for primary and secondary stimulus activity we examined the effects of stimulus type (faces or scenes), time period (encoding or delay), condition (ND, ED or DD) and task

(remember/ignore or passive view). When examining differences between sub-groups (eg. those with high and low performance), group was added as an additional factor.

Our approach was to use activity associated with face and scene stimuli (within Fusiform Face Areas (FFA) and Parahippocampal Place Area (PPA) respectively) as a tool to investigate modulation of attention. As such, our focus was not on differences between face and scene processing per se, but on the effects of task and interactions between task and distraction condition. With a separate behavioral study we observed that the performance cost of distraction (specifically DD) reached significance when participants were asked to remember scenes and ignore faces ( $F(2,82) = 6.883, p = 0.002$ ) but not when they were asked to remember faces and ignore scenes ( $F(2,82) = 0.080, p = 0.923$ ). Furthermore, others have restricted their analysis to left PPA activity, describing this as “the most robust marker of modulation identified in young adults”<sup>8</sup>. However, we observed the same pattern of results for suppression and enhancement in FFA and PPA, which was supported by the statistical analyses (there were no significant interactions between stimulus type and task, or between stimulus type, task and distraction condition, as described in the Supplementary Notes). Therefore, we included “stimulus type” in the ANOVAs we report, but averaged across stimulus type for the t-tests the figures. For completeness, results for each ROI are reported in the Supplementary Figure 1.

## Results

For each participant, behavioral responses during scanning were used to establish how much information was held in WM for each task and distraction condition, using the K-value<sup>1,13</sup>. Adding distractors during the encoding period did not significantly impair WM performance (paired t-test comparing ND and ED:  $t(21) = -0.147, p = 0.885$ ), but adding distractors during the delay period did ( $F(2,42) = 5.990, p = 0.005$ ; paired t-tests comparing ND and DD conditions:  $t(21) = 3.042, p = 0.006$ ; ED and DD conditions:  $t(21) = 2.660, p = 0.015$ ).

Despite impaired performance associated with the DD condition, and the varying duration of the delay period, we were concerned that participants may avoid seeing the DD by closing their eyes during the delay period. Therefore, using different participants we examined eye closure during the delay period of the task. These were of the extremely short duration of 127.049ms ( $SD = 44.675ms$ ) when remembering faces and 131.806ms ( $SD = 36.800ms$ ) when remembering scenes, during a delay period of 3s. Furthermore, the likelihood of eye-closure and the duration of eye-closure did not differ between situations where distractor stimuli were present or absent (remembering faces:  $F(1.205,27.720) = 1.088, p = 0.346$ , Huynh-Feldt correction; remembering scenes:  $F(2,46) = 0.340, p = 0.714$ ) and remembering faces:  $F(1.433,32.963) = 1.277, p = 0.282$ , Huynh-Feldt correction; remembering scenes:  $F(1.535,35.311) = 0.835, p = 0.414$ ) respectively).

### Primary Stimulus activity (“enhancement”)

We considered primary stimulus activity using FFA and PPA activity from blocks in which they were faces and scenes respectively (see Supplementary Figures 1a and b and Supplementary Note 1 for separate analysis of FFA and PPA activity). As anticipated, there was greater primary stimulus activity during the encoding period (when the primary stimuli were displayed) than the delay period (when they were absent) (main effect of time period:  $F(1,21) = 161.45$ ,  $p < 0.001$ , Figure 2a), for each condition and task (paired t-tests comparing the encoding and delay periods:  $p < 0.01$ ). Importantly, we also observed greater primary stimulus activity when primary stimuli were to be remembered compared to passive view, and this enhancement was specific to the encoding period (interaction between task and time period:  $F(1,21) = 31.214$ ,  $p < 0.001$ ; main effect of task for the encoding period:  $F(1,21) = 18.811$ ,  $p < 0.001$ , and for the delay period:  $F(1,21) = 0.406$ ,  $p = 0.531$ ). The enhancement was observed for each condition (paired t-tests between tasks:  $p < 0.05$ ), and did not differ between conditions (interaction between task and condition for the encoding period:  $F(2,42) = 0.971$ ,  $p = 0.387$ ).

#### Secondary stimulus activity (“suppression”).

We considered secondary stimulus activity, using FFA and PPA activity from blocks in which the secondary stimuli were faces and scenes respectively (see Supplementary Figures 1c and d and Supplementary Note 2 for separate analysis of FFA and PPA activity).

The suppression effect reported previously, using different paradigms<sup>eg. 5,8,6</sup>, was a reduction in activity when stimuli were to be ignored compared to passive view with the same stimuli. For our paradigm that would correspond to a task difference (remember/ignore task < passive view) within the ED and DD conditions. However, for our paradigm we did not observe a significant task difference for the ED condition (encoding period:  $t(21) = -0.685$ ,  $p = 0.501$ ; delay period:  $t(21) = 0.305$ ,  $p = 0.764$ ) or the DD condition (encoding period:  $t(21) = 1.341$ ,  $p = 0.194$ ; delay period:  $t(21) = 0.057$ ,  $p = 0.955$ ).

#### Encoding Distraction

We did observe a different suppression effect: a significant interaction between condition and task for the encoding period ( $F(1.669,42) = 3.487$ ,  $p = 0.049$ , Huynh-Feldt correction) but not the delay period ( $F(2,42) = 1.017$ ,  $p = 0.370$ ). Further ANOVAs revealed that this interaction was specific to the ND and ED conditions ( $F(1,21) = 4.961$ ,  $p = 0.037$ ). Unsurprisingly, for the passive view task, there was a significant increase in secondary stimuli activity when these stimuli were added to the display (paired t-test between ND and ED:  $t(21) = -4.381$ ,  $p < 0.001$ ). However comparing these same conditions for the “remember/ignore” task (with identical stimuli, but now the primary stimuli were to be remembered and the secondary stimuli ignored) we did not see a difference in secondary stimuli activity ( $t(21) = -1.094$ ,  $p = 0.286$ ). The significant increase in activity associated with presenting secondary stimuli during passive view was not seen when these stimuli were to be ignored. In this sense, activity associated with secondary stimuli was “suppressed”, although here the suppression is the absence of an increase in activity associated with stimulus presentation, rather than a reduction in activity when the stimuli are to be ignored compared to passive view.

Our findings also showed that during the encoding period, when there was no overt distraction and participants were asked to remember faces or scenes, there was a significant increase (enhancement) relative to passive view not only in regions associated with the stimuli which were to be remembered (FFA and PPA respectively;  $t(21) = 4.254$ ,  $p < 0.001$ ) but also in regions associated with the other stimulus type (PPA and FFA respectively), even though no stimuli of that type were displayed ( $t(21) = 3.408$ ,  $p = 0.003$ ). However, when that other stimulus type should be ignored (ED), the enhancement was specific to the stimuli that should be remembered, and activity associated with the other stimulus type was no greater than when those stimuli were passively viewed ( $t(21) = -0.685$ ,  $p = 0.501$ ).

### Delay Distraction

For the delay period, there was greater secondary stimulus activity in the DD condition (when those stimuli were displayed), regardless of whether they should be passively viewed or ignored (main effect of condition:  $F(2,42) = 10.951$ ,  $p < 0.001$ ; paired t-tests (averaging across task): DD > ND,  $t(21) = -4.791$ ,  $p < 0.001$  and DD > ED,  $t(21) = -3.314$ ,  $p=0.003$ ). Unlike the encoding period, for the delay period there was no significant interaction between condition and task ( $F(2,42) = 1.017$ ,  $p = 0.370$ ), so no evidence of the suppression effect we had observed for ED during the encoding period (see Supplementary Note 5 for additional analysis).

### Comparison between suppression for ED and DD across the whole group

Having observed a significant suppression effect (although different to that previously reported) for ED (during the encoding period), but not DD (during either time period), we directly compared the effect of ED during encoding and DD during the delay period. We adapted the ANOVA to consider two distraction conditions (ND and ED for the encoding period; ND and DD for the delay period). The difference in the “suppression” effect between ED and DD did not reach statistical significance (interaction between time, distraction condition and task:  $F(1,21) = 1.578$ ,  $p = 0.223$ ). However, when considering FFA and PPA activity separately, we observed a significant difference for FFA secondary stimulus activity ( $F(1,21) = 4.653$ ,  $p = 0.043$ ), but not for PPA activity ( $F(1,21) = 0.046$ ,  $p = 0.833$ ) (see below for further comparisons between ED and DD), perhaps a consequence of faces being more distracting, in line with the results from our separate behavioral study, described above. These results suggest that the suppression effect is specific to ED.

### Distractor Filtering Ability

With the same participants that took part in the scanning tasks, we conducted a behavioral experiment outside of the scanner to establish each participant's ED and DD filtering ability and WMC. The procedure was the same as that used for the scanning task, except that the stimuli were circles presented in different positions on 16 position circular grid <sup>see 2</sup>. Participants were asked to remember the positions of four or five red circles in the WMC task (with no overt distraction), and three red circles in the ND, ED and DD conditions. In the ED and DD conditions there were two yellow circles to ignore. All red circles were presented simultaneously, and during the response period a question mark was shown in one of the grid

positions, prompting participants to indicate, via a button press, whether there had been a red circle in that position. K-values were obtained for each condition and for the WMC task. The residuals from the regression equation  $ED = a + \beta DD$  were used as a measure of ED filtering ability and the residuals from the equation  $DD = a + \beta ED$  were used as a measure of DD filtering ability. This approach allowed us to control for variance associated with WM storage and instructions relating to which stimuli were to be remembered/ignored. The measures did not significantly correlate ( $r = -0.330, p = 0.144$ ). For each measure a median split was used for comparisons between participants high and low ED filtering ability and high and low DD filtering ability.

### Enhancement and ED/DD filtering ability

Those with high ED filtering ability showed greater enhancement of primary stimulus activity than those with low ED filtering ability for the ND condition (interaction between group, condition and task:  $F(2,36) = 3.893, p = 0.029$ ; for ND: interaction between group and task:  $F(1,18) = 6.571, p = 0.020$ ). This was significant for both the encoding period ( $F(1,18) = 5.965, p = 0.025$ ; Figure 3a) and the delay period ( $F(1,18) = 5.749, p = 0.028$ ; Figure 3c) (see Supplementary Figures 2a and b for primary stimulus activity in all conditions, and Supplementary Note 3). Furthermore, for both time periods, there was a significant correlation between enhancement in the ND condition and ED filtering ability (Figures 3e and g), which was driven by a significant negative correlation between ED filtering ability and primary stimulus activity for the passive view rather than the remember/ignore task (Figures 3i and k).

Whereas greater enhancement was seen in those with *higher* ED filtering ability, for DD filtering ability, greater enhancement was associated with *lower* filtering ability, and again this was specific to the ND condition (interaction between group, condition and task:  $F(2,34) = 5.824, p = 0.007$ ; ND: interaction between group and task:  $F(1,17) = 11.127, p = 0.004$ ) (see Supplementary Figures 2c and d for all conditions, and Supplementary Note 4). Again this was seen for both the encoding period ( $F(1,17) = 7.540, p = 0.014$ , Figure 3b) and the delay period ( $F(1,17) = 11.702, p = 0.003$ ; Figure 3d). The correlation between enhancement in the ND condition and DD filtering ability reached statistical significance only for the delay period (Figure 3g), and was driven by a positive association between DD filtering ability and primary stimulus activity for the passive view task (Figure 3k).

Across all participants enhancement at ND did not predict WMC (measured prior to scanning,  $r = 0.347, p = 0.123$ ). However, as we had observed a positive association with ED filtering ability, but a negative association with DD filtering ability, we split the group according to whether ED filtering ability was greater than DD filtering ability or vice versa. For the ED > DD group, greater enhancement in the encoding period of the ND condition predicted greater WMC ( $r = 0.602, p = 0.038$ ), which was driven by an association between WMC and primary stimulus activity in the remember task ( $r = 0.621, p = 0.031$ ) rather than the passive view task ( $r = -0.113, p = 0.726$ ) (Figure 5). For the DD > ED group, WMC was not predicted by enhancement during ND ( $r = 0.092, p = 0.814$ ), but was predicted by ED filtering ability ( $r = 0.686, p = 0.041$ ; for the ED > DD group this was not the case:  $r = 0.132, p = 0.681$ ).

### Suppression and ED/DD filtering ability

Having observed significant associations between primary stimulus activity and both ED and DD filtering ability, we considered secondary stimulus activity. There was no evidence of a difference in suppression between those with high and low ED filtering ability ( $p > 0.1$  for interactions between group and the factors time, condition and task). However, for those with high DD ability, but not low DD ability, there was a significant suppression effect which was specific to the encoding period (interaction between time period, condition, task and group:  $F(2,34) = 3.500$ ,  $p = 0.041$ ; interaction between time, condition and task for high DD filtering ability:  $F(2,18) = 18.564$ ,  $p < 0.001$ ; for low DD filtering ability:  $F(2,16) = 0.397$ ,  $p = 0.679$ ; for high DD filtering ability and the encoding period: interaction between condition and task:  $F(2,18) = 12.498$ ,  $p < 0.001$ , and for the delay period:  $F(2,18) = 0.523$ ,  $p = 0.602$ ). This was driven by a difference between ND and ED conditions specifically for the passive view task (main effect of condition for the passive view task:  $F(2,18) = 13.250$ ,  $p < 0.001$ , and for the remember/ignore task:  $F(2,18) = 1.082$ ,  $p = 0.360$ ; paired t-tests showed ED > ND:  $t(9) = -0.694$ ,  $p < 0.001$ , ED > DD:  $t(9) = 3.325$ ,  $p = 0.009$ , ND and DD did not significantly differ:  $t(9) = -0.694$ ,  $p = 0.505$ ). Therefore the suppression effect we had seen for the whole group was evident for those with high DD ability, but not those with low DD ability. Furthermore, for this group there was also a significant task difference within the ED condition (paired t-test:  $t(9) = -5.138$ ,  $p = 0.001$ ), in line with the suppression effect reported previously. Importantly, for this group there was also a significant difference between suppression of ED during encoding and suppression of DD during the delay period (interaction between time, distraction condition (ND compared to ED for the encoding period and ND compared to DD for the delay period) and task:  $F(1,9) = 5.809$ ,  $p = 0.039$ ), adding further support to the suppression effect being specific to ED.

## Discussion

We observed enhancement of stimulus specific cortical activity when stimuli were to be remembered, compared to passive view, which did not significantly differ when distractors were added during encoding or during maintenance. Furthermore, in the absence of overt distraction such enhancement separately predicted an individual's ability to ignore distraction during encoding (a positive association) and during maintenance (a negative association). We also observed that adding task irrelevant stimuli to the display during encoding increased cortical activity associated with those additional stimuli during passive view, but not when participants were asked to ignore those stimuli and remember other stimuli. We observed such suppression for distraction presented during encoding, but not for distraction presented during maintenance. However, suppression at encoding was greater for individuals with high DD filtering ability. Our findings reveal common and distinct mechanisms for ignoring distractors during encoding and maintenance, and the associations with filtering performance highlight links between enhancement/suppression at encoding and filtering ability at both encoding and during maintenance. The present results therefore reveal specific neural mechanisms by which relevant information is remembered and irrelevant information is ignored, which contribute to intra-individual differences in WM performance.

Previously the approach has been to compare a remember/ignore task condition to a stimulus- matched passive view condition. With that approach, reduced activity has been reported when stimuli were to be

ignored compared to passive view, which we did not observe across the group.

There are several important differences between our ED condition and those for which reduced activity when ignoring distraction compared to passive view has been reported. Some of those studies involved sequential presentation of task relevant and irrelevant stimuli, in a randomized order, with task relevance only becoming apparent when each stimulus is displayed <sup>eg.5,8,14</sup>. Others have used sequential presentation of superimposed face and scene stimuli, which require the participant to switch between “seeing” a face or a scene<sup>6</sup>. For our study, task relevant stimuli were presented simultaneously, to allow us to interrogate the distinction between ED and DD. Furthermore, participants knew the task relevance of upcoming stimuli in advance (for the remember/ignore task there were always two stimuli to remember in the ND condition, two stimuli to remember and two stimuli to ignore during ED, and two stimuli to remember, followed by two stimuli to ignore in the DD condition). Furthermore, when both task relevant and irrelevant stimuli were presented simultaneously (ED), the task relevant and irrelevant stimuli were spatially distinct. It is therefore possible that the suppression reported previously represents a wide-spread reduction of activity associated with the whole display, or of items that span the whole display, when these are deemed to be task irrelevant, and that our paradigm requires a more spatially-selective approach.

Another possibility is that the lower activity associated with ignoring stimuli compared to passive view reported previously does not represent a reduction of activity when these stimuli are to be ignored, but is instead a consequence of an increase in distractor-related activity when these stimuli are presented and passively viewed, and an absence of such an increase when they are presented but ignored. We were able to observe this absence of an increase for the ignore task as we had data from task-matched conditions in which there was no overt distraction (ND). Although we did not see reduced activity when ignoring distractors compared to passive view across the whole group, this was observed for the sub-group of individuals with high DD filtering ability. For this sub-group, comparison with the no distraction conditions revealed that a significant difference was seen only for the passive view task (ED > ND), not the remember/ignore task. Therefore, although we do observe the previously reported suppression effect for this sub-group, we have no evidence for this representing a reduction in activity when those stimuli are to be ignored, only for a significant increase in activity when those stimuli were added to the display during the passive view task, which is not seen for passive view.

The suppression effect we observed between ND and ED conditions during encoding was not evident between ND and DD conditions, for either time period, consistent with the previous finding of no difference in FFA activity to faces that were ignored and passively viewed during the delay period<sup>15</sup>. One possibility is that distractor suppression is involved in resolving perceptual competition between relevant and irrelevant stimuli when these are presented together (ED <sup>see 16</sup>), but not when these are presented separately (DD). With a task in which relevant stimuli were sequentially presented, we previously observed evidence of competition whereby a stimulus representation held in WM was susceptible to competition when a second stimulus is perceived<sup>17</sup>. However, the demand for competition resolution may be less for

DD than ED, or separate mechanisms may be involved in resolving each type of competition. Furthermore, other potential mechanisms for ignoring DD have been identified, for example ignoring delay distraction has been associated with changes in functional-connectivity between visual association area and middle frontal gyrus<sup>15</sup>, as well as DLPFC control over representations of task-relevant items<sup>18</sup>, and a functional coupling of visual cortical areas associated with irrelevant information to the default-network<sup>6</sup>.

Our data also revealed significant correlations between enhancement and both ED and DD filtering performance. To the best of our knowledge this shows for the first time an association between individual differences in enhancement and performance during WM (although greater P3 enhancement has been associated with higher WM accuracy and faster response times<sup>19</sup>. A link between enhancement and performance had been identified when an increase in WM load lead to both poorer WM performance and diminished enhancement<sup>5</sup>. Here greater enhancement in the no distraction condition was associated with higher ED filtering ability, but lower DD filtering ability.

These associations did not reach significance for conditions in which distractors are presented, perhaps because distractors were sometimes unnecessarily encoded into WM see <sup>1,2</sup>, consistent with reports of diminished enhancement when both faces and scenes should be remembered<sup>5</sup>.

The difference in the direction of the association we observe between enhancement and ED filtering ability (positive) and between enhancement and DD filtering ability (negative) supports an interplay between ED and DD filtering, and extends our previous behavioral findings<sup>12</sup>. In that study DD filtering showed greater decline than ED filtering with increasing age but ED filtering performance became more predictive of WM in the absence of overt distraction, especially for older adults with poorer DD filtering ability. We speculated that those with low DD filtering may compensate with more focused attention at encoding, perhaps employing ED filtering mechanisms even when there is no overt distraction. Our present finding of greater “enhancement” for individuals with lower DD filtering ability, when there is no overt distraction, provides a potential mechanism for this compensation. Furthermore, the association between enhancement and ED filtering ability indicates that enhancement benefits encoding, and does so with mechanisms that support ED distractor filtering. Although we found no evidence for a specific suppression mechanism associated with ignoring DD, our findings do indicate that the contribution of enhancement and suppression during encoding determines the extent to which representations are buffered from future distraction.

All three of the associations we saw with filtering ability were driven by associations with activity in the passive view task, not the remember/ignore task, consistent with reports of neural measures during “rest” predicting cognitive task performance, supporting their functional role in preparing for a cognitive challenge<sup>20</sup>. It is also possible that those with poor filtering ability were unnecessarily directing cognitive resources to, and perhaps even remembering, the stimuli presented in the passive view condition<sup>1</sup>.

Given that ED and DD filtering ability differentially predicted enhancement, we performed exploratory analysis, splitting the group according to whether ED filtering ability was superior (9 participants) or

inferior (12 participants) to DD filtering ability. For those with superior ED filtering ability, who presumably would have benefited from the compensation mechanism described above, greater “enhancement” in the ND condition predicted greater WMC. For participants with superior DD filtering ability, WMC was instead predicted by ED filtering ability, in line with ED filtering, rather than compensatory enhancement, being the “limiting factor”.

In summary the present results reveal specific neural mechanisms by which enhancement and suppression of cortical activity support an individual’s ability to ignore distraction at different stages of WM and could contribute to an individual’s WMC.

## Methods

### Participants

Thirty-two healthy participants (right handed) gave informed consent to participate in the study, which was approved by York Neuroimaging Centre’s ethics committee. Datasets were excluded when accuracy was equal to or below 50% for any block (7 participants). After collecting data from 21 participants, we added practice trials prior to scanning, and feedback on accuracy after each block. Data from three further participants were omitted due to a technical error displaying the stimuli, excessive movement, and poor performance out of the scanner.

fMRI data from 22 participants (13 females, ages 18-29) and out of scanner behavioural data from 21 participants (one dataset was lost due to a technical error) were analysed.

### Tasks and stimuli

Each participant completed two scanning sessions. The first included the ND blocks for each task and stimulus type (four blocks, with the order counterbalanced) as well as the functional localiser scan. The second session included the remaining seven blocks, with order counterbalanced.

Greyscale images of natural scenes and faces with neutral expressions were used (these images had also been used by Gazzaley et al.<sup>5,8</sup>). For each of the 11 blocks, the same set of face and scene images (subtending a visual angle of 6.92° horizontally and 6.46° vertically) were used, with no repetitions within a block. For each block there were two primary stimuli, each presented in a pseudo-randomly selected quadrant of the screen. When secondary stimuli were shown they were in the remaining quadrants. All other quadrants were grey (Figure 1). For the remember/ignore task, a single, centrally presented image from the primary stimulus category, was shown during the response period, prompting participant to indicate, via a button press, whether it matched one of the primary stimuli from the encoding period, which it did for half of the trials. For the passive view task, participants were asked to indicate whether an arrow pointed to the left (which it did for half the trials) or to the right. For each block there were 24 of the trials described, and an additional six trials in which a white fixation cross was presented instead of a

response period, to help de-correlate the regressors associated with the response period from regressors associated with other parts of the trial.

For the functional localiser scan, centrally presented single images (112 faces and 112 scenes) were presented sequentially for 1.4s each. Faces and scene blocks (each with 16 images) were presented in pairs, with 22.4s in between each pair. Participants performed a 1-back task, pressing a button if they identified a match (which it did for 28 images).

Prior to entering the scan room, participants completed two visuo-spatial WM tasks <sup>see 2</sup>. Red circles were presented simultaneously for 1s on a circular grid of 16 squares, there was a delay period of 3s, then a question mark was shown at one of the grid positions, asking participants to indicate with a button press whether there had been a red circle in that position (which there had for half of the trials). To obtain a measure of WMC (without overt distraction) four or five red circles were shown (40 trials). To obtain measures of ED and DD filtering, three red circles were shown in ND, ED and DD conditions (each with 30 trials). Distractors were two yellow circles.

### MRI acquisition

Imaging data were collected using a 3.0 Tesla MRI scanner (Siemens) with a 20-channel phased-array head coil and a bottom up interleaved echo planar imaging (EPI) sequence. For the experimental scan: TR = 2.1s, TE = 30ms, flip angle = 80 degrees, FOV = 192x92x108mm, matrix size = 64x64, number of volumes = 213, voxel size = 3x3mm, slice thickness = 3mm with no inter-slice gap and 36 slices were acquired. For the functional localiser scan: TR = 2s, TE = 30ms, flip angle = 80 degrees, FOV = 192x192x108mm, matrix size = 64x64, number of volumes = 227, voxel size = 3x3mm, slice thickness = 3mm with no inter-slice gap and 36 slices were acquired. A T1-weighted structural image was obtained for each participant (TR = 2.3s, TE = 2.26ms, flip angle = 8 degrees, FOV = 256x256, voxel size = 1x1, slice thickness = 1mm, number of slices = 176) and a T1-weighted FLAIR image (TR = 3s, TE = 8.6ms, flip angle = 150, FOV = 192x192mm, matrix size = 256 x 256, voxel size = 0.75x0.75mm, slice thickness = 3.0mm, number of slices = 36) was taken in the same plane as the EPI data, for co-registration of the functional data to the structural image.

### Data analysis

For data processing FEAT (fMRI expert analysis tool) version 6.0 part of FSL (FMRIB's Software Library, [www.fmrib.ox.ac.uk/fsl](http://www.fmrib.ox.ac.uk/fsl)) was used. The data were skull stripped using BET (Brain extraction tool)<sup>21</sup>, motion corrected using MCFLIRT<sup>22</sup>, slice time corrected using fourier-space-time-series phase-shifting and non-brain removal using BET<sup>21</sup> and spatially smoothed using a Gaussian Kernel of FWHM (full width at half maximum) 8mm and high pass temporal filtering (Gaussian-weighted least-squares straight line fitting, with sigma = 100s). Registration of the fMRI data to the structural data and standard brain (MNI152 2mm) was carried out using FLIRT<sup>23,22</sup>. Registration from structural data to the standard brain was further refined using FNIRT<sup>24,25</sup>.

A time-series statistical analysis was carried out using FILM with local autocorrelation correction<sup>26</sup>. The general linear model included regressors for the encoding period (3,4 or 5s), delay period (5,7 or 9s), and the response period (2s). Only correct trials were analysed and there was an additional regressor for incorrect trials. Regressors were convolved with a single gamma hemodynamic response function.

The scene-sensitive PPA and face-sensitive FFA ROIs were defined using data from the functional localiser scan, and the contrasts: scenes > faces and faces > scenes respectively. For each contrast the maximally active voxel within the respective anatomical region, in each participant's native brain space, was selected. Two voxels were added to the peak voxel in the x, y and z directions, making a ROI of 7 contiguous voxels. For each time period, and each block we extracted the parameter estimates and calculated percent signal change for each participant. These data were analysed using IBM SPSS Statistics version 25. The accompanying P values were determined by two tailed analysis and considered significant if p < 0.05.

## Declarations

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### Author Contributions

FM, CA and AG designed the tasks together. CA and AG prepared the experiments. CA and MG conducted the experiments. CA, AG and FM analysed the data. FM and CA wrote the manuscript and ST and TZ provided revisions.

Thirty-two healthy participants (right handed) gave informed consent to participate in the study, which was approved by York Neuroimaging Centre's ethics committee.

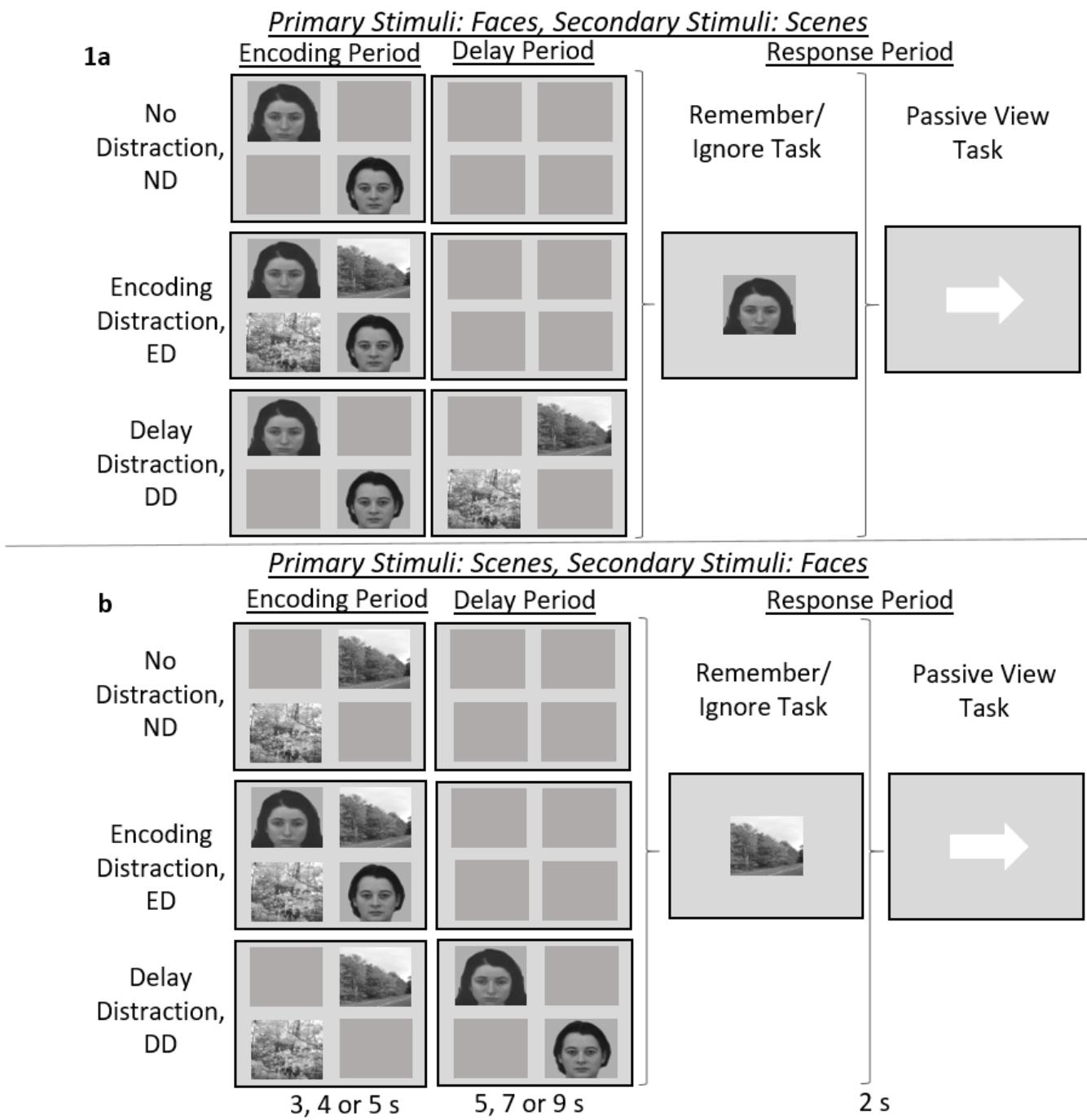
## References

- 1 Vogel, E.K., McCollough, A.W., Machizawa, M.G. Neural measures reveal individual differences in controlling access to working memory. *Nature*, **438**, 500-503 (1998)
- 2 McNab, F., Klingberg, T. Prefrontal cortex and basal ganglia control access to working memory. *Nature Neuroscience*, **11**, 103-107 (2008)
- 3 Hasher, L., Zacks, R.T. Working memory, comprehension, and aging: A review and anew view. *The Psychology of Learning and Motivation*, ed Bower, G.H. (Academic, San Diego), Vol **22**, 193–225 (1988)

- 4 Lee, F-Y., Cowan, N., Vogel, E.K., Rolan, T., Valle-Inclán, F., Hackley, S.A. Visual working memory deficits in patients with Parkinson's disease are due to both reduced storage capacity and impaired ability to filter out irrelevant information. *Brain*, **133**, 2677-2689 (2010)
- 5 Gazzaley, A., Cooney, J.W., McEvoy, K., Knight, R.T., D'Esposito, M. Top-down enhancement and suppression of the magnitude and speed of neural activity. *J Cog Neuro*, **17**, 507-517 (2005)
- 6 Chadick, J.Z., Gazzaley, A. Differential coupling of visual cortex with default network or frontal- parietal network based on goals. *Nat Neurosci*, **14**, 830-832 (2012)
- 7 Rutman, A.M., Clapp, W.C., Chadick, J.A. & Gazzaley, A. [Early top-down control of visual processing predicts working memory performance](#). *J Cogn Neurosci*, **22**(6), 1224-34 (2010)
- 8 Gazzaley, A., Cooney, J.W., Rissman, J., D'Esposito, M. Top-down suppression deficit underlies working memory impairment in normal aging. *Nat Neurosci*, **8**, 1298-1300 (2005).
- 9 Chadick, J.Z., Zanto, T.P. & Gazzaley, A. Structural and functional differences in prefrontal cortex underlie distractibility and suppression deficits in ageing. *Nature Commun*, **5**, 4223 (2014)
- 10 Gazzaley, A., Clapp, W., McEvoy, K., Knight, R., D'Esposito, M. [Age-related top-down suppression deficit in the early stages of cortical visual memory processing](#), *Proc Natl Acad Sci*, **105**(35), 13122- 13126 (2008)
- 11 McNab, F., Dolan, R.J. Dissociating distractor-filtering at encoding and during maintenance. *JEP: HPP*, **40**, 960-967 (2014)
- 12 McNab, F., Zeidman, P., Rutledge, R.B., Smittenaar, P., Brown, H.R., et al. Age-related changes in working memory and the ability to ignore distraction. *PNAS*, **112**, 6515-6518 (2015)
- 13 Cowan, N. The magical number 4 in short-term memory: a reconsideration of mental storage capacity. *Behav Brain Sci*, **24**, 87-185 (2001)
- 14 Zanto, T.P. & Gazzaley, A. Neural Suppression of Irrelevant Information Underlies Optimal Working Memory Performance, *J Neurosci*, **29**(10), 3059-3066 (2009)
- 15 Clapp, W.C., Rubens, M.T., Gazzaley, A. Mechanisms of working memory disruption by external interference. *Cerebral Cortex*, **20**, 859-872 (2010)
- 16 Desimone, R. & Duncan, J. Neural mechanisms of selective visual attention. *Annu. Rev. Neurosci.* **18**, 193-222 (1995)
- 17 Ahmad, J., Swan, G., Bowman, H., Wyble, B., Nobre, A.C., Shapiro, K., McNab, F. Competitive interactions affect working memory performance for both simultaneous and sequential stimulus presentation. *Scientific Reports*, **7**, 4785 (2017)

- 18 Feredoes, E., Heinen, K., Weiskopf, N., Ruff, C., Driver, J. Causal evidence for frontal involvement in memory target maintenance by posterior brain areas during distractor interference of visual working memory. *Proc Natl Acad Sci*, **108**, 17510–17515 (2011)
- 19 Padgaonkar, N.A., Zanto, T.P., Bollinger, J. & Gazzaley, A. Predictive cues and age-related declines in working memory performance. *Neurobiol. Aging*, **49**, 31–39 (2017)
- 20 Sala-Llonch, R. Bartrés-Faz, D. & Junqué, C. Reorganization of brain networks I aging: a review of functional connectivity studies. *Front Psychol*, **6**, 663 (2015)
- 21 Smith, S. M. Fast robust automated brain extraction. *Human Brain Mapping*, **17**, 143–155 (2002)
- 22 Jenkinson, M., Bannister, P., Brady, M., & Smith, S. Improved optimization for the robust and accurate linear registration and motion correction of brain images. *NeuroImage*, **17**, 825–841 (2002)
- 23 Jenkinson, M., & Smith, S. A global optimisation method for robust affine registration of brain images. *Medical Image Analysis*, **5**, 143–156 (2002)
- 24 Andersson, J. L. R., Jenkinson, M., Smith, S. Non-linear registration aka Spatial normalisation FMRIB Technical Report TR07JA2. FMRIB Analysis Group of the University of Oxford, 1–22. (2007)
- 25 Andersson, J. L. R., Jenkinson, M., Smith, S., *Non-linear optimisation*. FMRIB technical report TR07JA1. (2007)
- 26 Woolrich, M. W., Ripley, B. D., Brady, M., & Smith, S. M. Temporal autocorrelation in univariate linear modeling of fMRI data. *NeuroImage*, **14**, 1370–1386 (2001)

## Figures



**Figure 1**

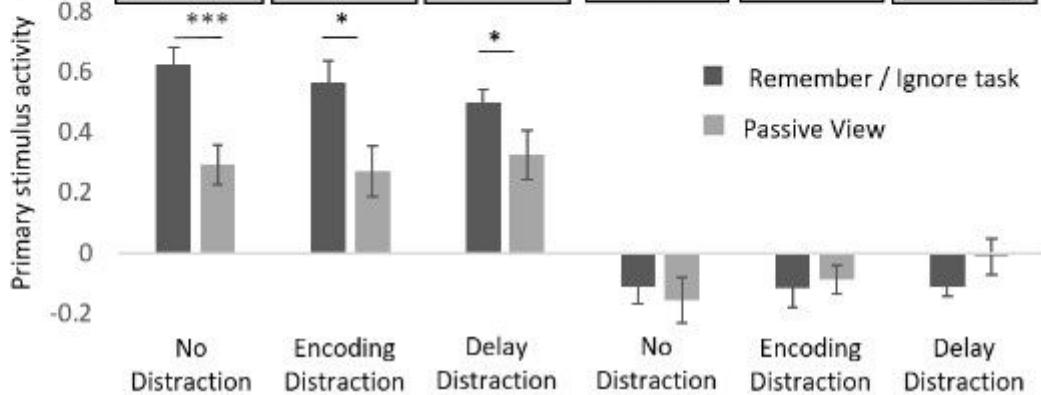
The three distraction conditions (No Distraction, Encoding Distraction and Delay Distraction) for the remember/ignore task, where primary stimuli (faces for a and scenes for b) were to be remembered and the secondary stimuli (scenes for a and faces for b) were to be ignored, and the stimulus-matched passive view task. Each combination of distraction condition and task was presented in a separate block (note that the ED passive view combination is shown in both a and b, but as the stimuli and task were identical, only one block was given, so there were 11 blocks in total).

2a

FFA: Remember Faces/  
Ignore Scenes or Passive View



PPA: Remember Scenes /  
Ignore Faces or Passive View

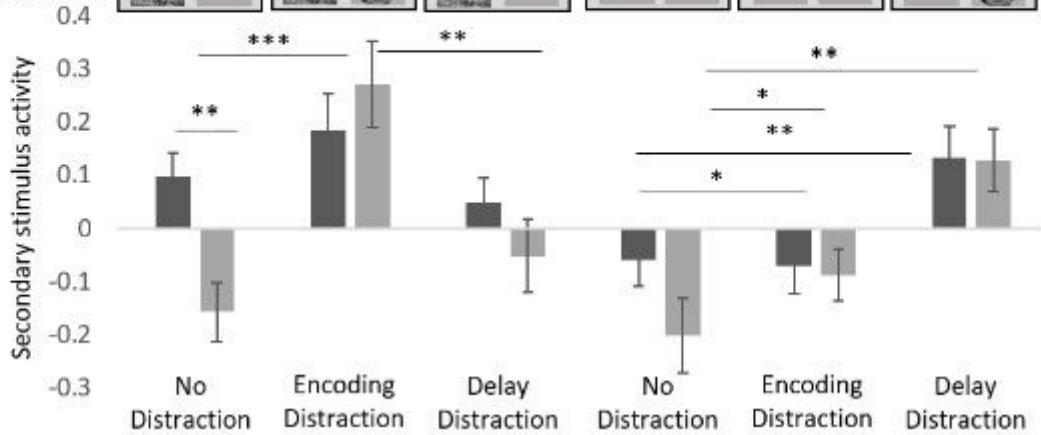


b

PPA: Remember Faces/  
Ignore Scenes or Passive View

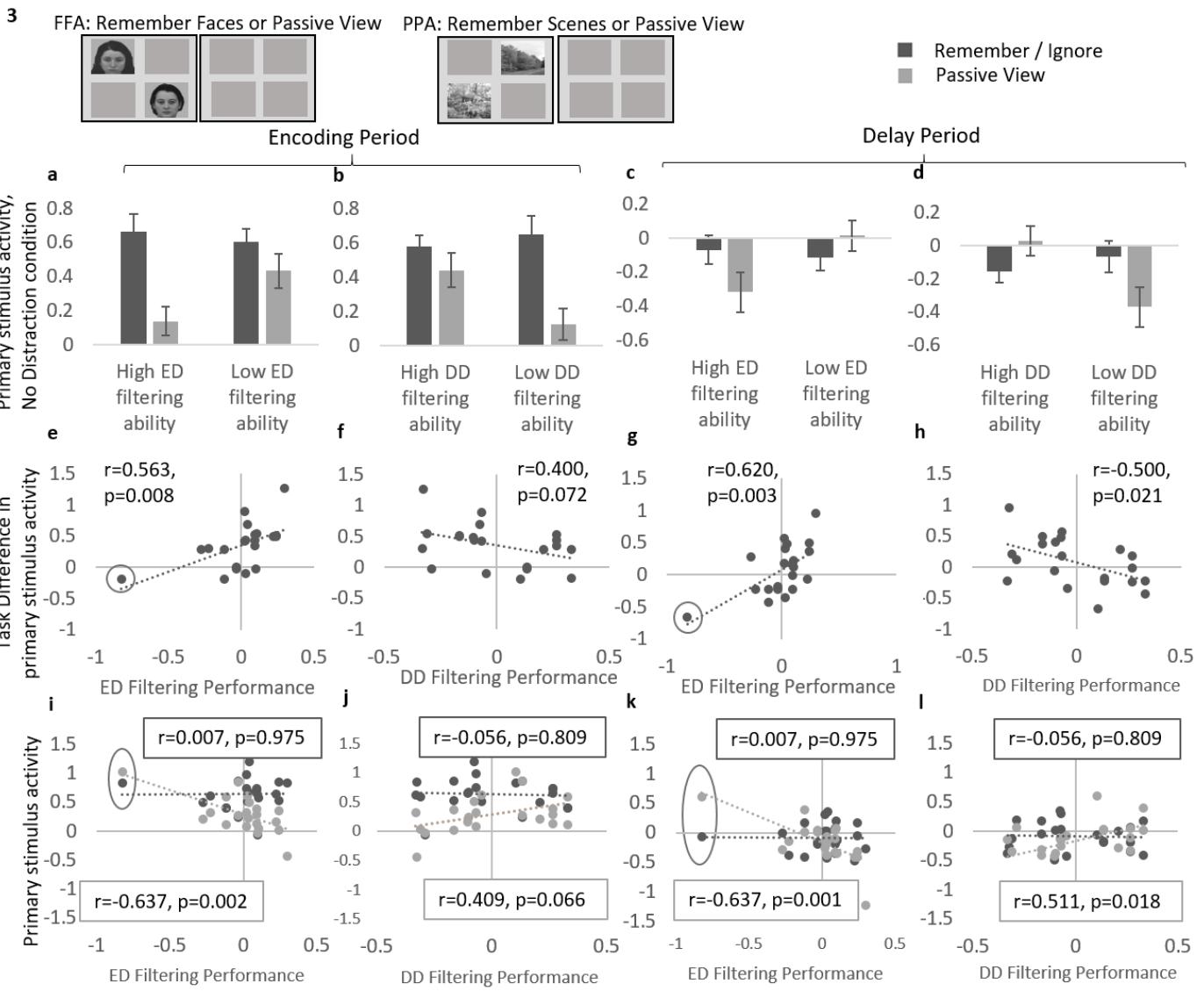


FFA: Remember Scenes /  
Ignore Faces or Passive View



**Figure 2**

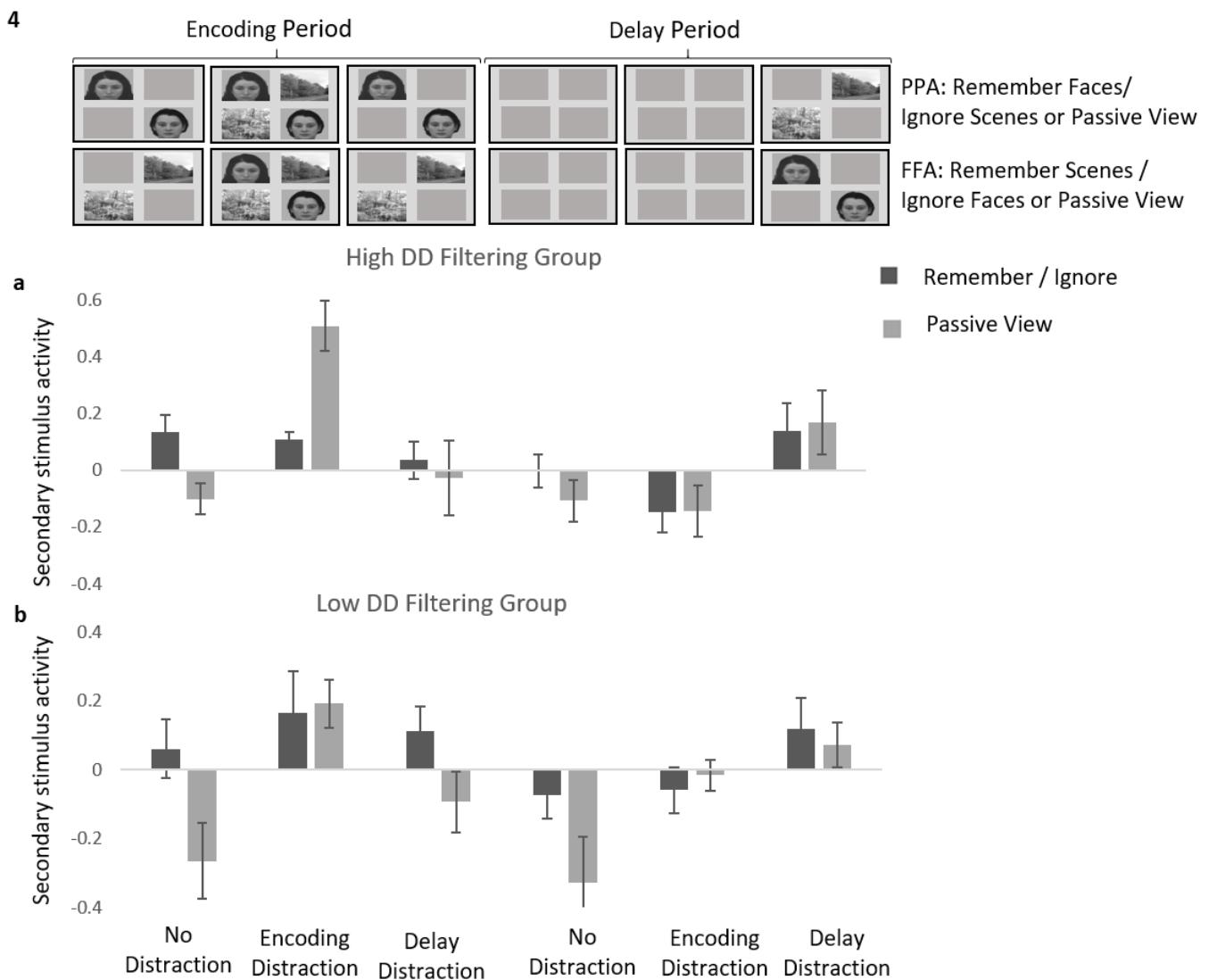
a) Primary stimulus activity and b) secondary stimulus activity for each task, condition and time period. The error bars indicate s.e.m. \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ .



**Figure 3**

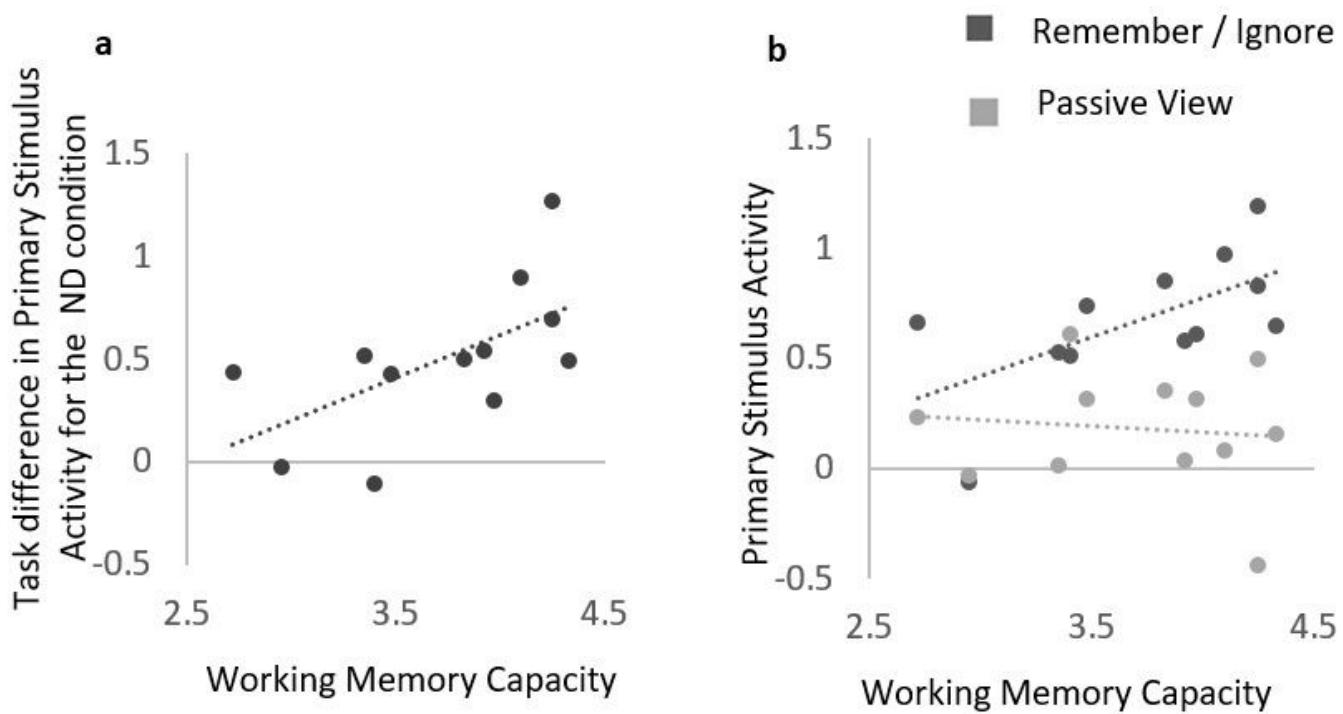
Primary stimulus activity for the No Distraction condition for those with high and low ED filtering ability, and those with high and low DD filtering ability for the encoding period (a and b respectively) and for the delay period (c and d respectively). e-h) Correlations between the task difference in primary stimulus activity (remember – passive view) during the encoding period of the No Distraction condition and either ED filtering ability (e), or DD filtering ability (f), and correlations between the task difference during the delay period of the No Distraction condition and either ED filtering ability (g) or DD filtering ability (h). Correlations between primary stimulus activity for the passive view or the remember task during the encoding period of the No Distraction condition and either ED filtering ability (i), or DD filtering ability (j), and correlations between primary stimulus activity for the passive view or the remember task during the delay period of the No Distraction condition and either ED filtering ability (k) or DD filtering ability (l). Due

to concern that the data points circled may be outliers, the analyses were re-run omitting this participant, but all results remained unchanged. The error bars indicate s.e.m.



**Figure 4**

Secondary stimulus activity for those with high and low DD filtering ability for each task, condition and time period. The error bars indicate s.e.m.



**Figure 5**

Correlations between working memory capacity and a) the difference in primary stimulus activity between the remember and the passive view tasks during the encoding period of the no distraction condition and b) primary stimulus activity in both the remember and passive view conditions, for participants with greater ED filtering ability than DD filtering ability.

## Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [SupplementaryInformation.pdf](#)