



Similar behaviour, different brain patterns: Age-related changes in neural signatures of ignoring

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ABSTRACT

We measured behavioural performance and fMRI activity whilst old and young adults performed a temporal segmentation task ('preview search'). Being able to select parts of the visual world to be attended or ignored is a critical visual skill. Both old and young adults were able to improve their performance on a difficult search task when some of the distracter items were presented earlier than the remainder. Comparisons of brain activity and functional connectivity, however, suggested that the underlying mechanisms are quite different for the two age groups. Older adults' activation patterns do not correspond to those predicted by simple increased involvement of frontal regions reflecting higher demand with age but seem to suggest that changes in brain activation patterns propagate throughout the cortex.

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Introduction

The visual field contains far more information than can usefully be processed at one time. Attention can separate the scene into those parts which are relevant to the current goal and those parts which are not. It can increase sensitivity to relevant parts of the scene (Carrasco et al., 2000; Posner et al., 1980; Yeshurun and Carrasco, 1999) and reduce processing of less important parts of the scene. Knowing the locations, identities or timing of distractions can improve performance (Folk and Remington, 1999; Ruff and Driver, 2006; Serences et al., 2004), for instance. The mechanisms underlying ignoring are not yet well understood. The segmentation of the scene into regions for attending and ignoring can be achieved via multiple cues including depth (Nakayama and Silverman, 1986), motion (McLeod et al., 1988), colour (Wolfe et al., 1989) and, the concern of this study, time (Watson and Humphreys, 1997).

It is likely that some image segmentation occurs automatically in a quick and bottom up manner. Segmentation by motion, for example, occurs even if the parietal cortex (involved in attention orienting) is disrupted by TMS (Ellison et al., 2007). On the other hand, some image segmentation requires deliberate effort. For instance, in the preview search paradigm, some distracters are presented earlier than the remainder and search target. Participants are able to ignore the first set of items and perform as if they are only searching the

second, newer, group – a benefit from preview (Watson and Humphreys, 1997). New items can be segmented from the old items by their temporal group or their onset time, both of which will help automatically segment the image (Donk and Theeuwes, 2001; Jiang et al., 2002; Mavritsaki et al., 2011). Evidence suggests that this segmentation by time is not an entirely automatic process. There is little benefit from the preview display, for instance, if attention or working memory is distracted: performing a secondary task whilst performing preview search reduces the benefit from preview (Humphreys et al., 2002). Furthermore, brain regions underlying successful benefit from preview overlap with those involved in visual working memory (Allen et al., 2008).

Here we ask whether older adults use the same processes to segment by time as younger adults. There are several reasons to suspect that older adults might be impaired at preview search compared to younger adults. First, there is an age-related decline in the ability to segment the image by spatial cues (Gilmore et al., 1985; Madden et al., 1996) and it is likely that there are shared processes underlying segmentation by time and segmentation by other cues (e.g. Dent et al., 2011). Second, older adults are typically worse at tasks which involve ignoring a set of distracters (Hasher et al., 1991). For instance, older adults show less negative priming. In this paradigm, a previously ignored item is responded to more slowly and less accurately when it subsequently becomes a target (May et al., 1995). This is attributed to the carry-over to the following trial of suppression applied to a distracter on the preceding trial, older adults may thus have weaker suppression of irrelevant distracters (Kane et al., 1997; Milliken et al., 1998). Third, whilst for young

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adults, activation in sensory regions for attended items increases and to ignored items decreases (compared to a neutral baseline), older adults show only the increases in activation for attended items (Gazzeley et al., 2005a,b). Finally, older adults have worse temporal resolution than younger adults (Andersen and Ni, 2008; Blake et al., 2008).

Despite these age related declines in suppressing distracters, temporal resolution and image segmentation, older adults seem to maintain their ability to benefit from preview in some circumstances. For instance, older adults were able to exclude previewed items from search when the new items could be segmented from the old items by both time and colour/form differences (Kramer and Atchley, 2000). When the old and new items were the same colour and shape, older adults still benefited from the preview but the benefit was reduced. Watson and Maylor (2002) similarly found that older adults could benefit from a preview display when old and new items were different shapes. They also found that older adults did not benefit from preview when the stimulus moved. Warner and Jackson (2009) found that older adults required the preview to be displayed longer than did younger adults. It seems, therefore, that older adults can exclude the previewed items, but their performance is less robust than that of younger adults. Since many of the mechanisms used by younger adults are degraded it is possible that different processes underlie the performance of older adults in preview search.

Perhaps it is unsurprising that older adults can sometimes benefit from the preview as in other paradigms they can benefit from other cues. Despite being slower at finding a target in a difficult search, when they can use colour to guide search, older adults' performance can match younger adults (Madden et al., 2002). Several authors have proposed that age-related declines in perceptual processes can be offset by increases in executive control processes in the prefrontal or frontal regions (Grady, 2000; Madden, 2007; Spreng et al., 2010) or more diffuse activity in these regions (Cabeza et al., 2002). The perceptual processes underlying the preview benefit appear to decline with age but older adults are still able to maintain some ability to benefit from preview. These theories predict that maintaining the benefit from preview will lead to increased activity in prefrontal or frontal regions in older, but not younger, adults. The preview paradigm, uniquely, allows us to measure both the preparation to ignore (in the first, preview) display as well as the consequences of any change in strategy with age. To pre-empt our results we find changes in connectivity in both the early and late phases of the task. We also find a distinctly different pattern of activation in older, compared to younger, adults, despite similar behaviour.

A second aim of this study was to investigate changes in visual cortex in response to the ignored previewed items. Several studies have found that distracters are processed differently in younger and older adults. On the one hand, there is evidence that older adults are less influenced by distracters. Gazzeley et al. (2005a,b) have shown a lack of modulation of brain activity for ignored items for older adults. Similarly, Kramer et al. (2006) found that older adults were less likely to return to already searched items (increased Inhibition of Return) than were younger adults. On the other hand, Madden et al. (2007a) presented search displays with either predictable targets or predictable distracters and compared them to displays where target and distracter identity changed on each trial. Young adults' performance was the same whether or not the distracters were varied and only decreased when the target was unpredictable. Older adults, on the other hand, were worse when either the distracter or the target was varied suggesting they could be influenced by the distracters. The preview search task allows us to measure responses to the initial previewed items directly (as they are on the screen alone). Benefit from preview has been linked to modulation of both category specific and retinotopic visual areas (Allen et al., 2008; Dent et al., 2011; Payne and Allen, 2011). If older adults process distracters less we may not see modulation of early visual areas. If, on

the other hand, older adults are more influenced by distracters we might see increases in activation in visually responsive regions.

Methods

Participants

39 participants took part in the study, recruited from the University of Birmingham participant pool. Participants in this pool take part in similar studies at the University on a regular basis. Older participants are screened for cognitive decline before joining the participant panel and are monitored informally for signs of decline. Participants who showed signs of memory loss or lack of ability to learn the task were excluded. Participants took part in exchange for a small cash payment or course credit (young only). Two younger participants and one older participant were excluded from further analysis because they showed no ability to use the preview display (in terms of any measure of performance) to aid search performance in either the practice or scanning sessions. Thus, only participants that we were confident could understand the instructions and attempt the task for the preview display were included. Two further older adults were excluded due to a failure to record behavioural responses in the scanner, and a further two old adults withdrew from the study. Thus, 17 old adults (11 females, 65–82 yrs old, $M=71.9$ years) and 15 young adults (9 females, 19–24 yrs old, $M=21.7$ years) remained in the analysis. All had normal or corrected-to-normal vision and gave written informed consent in accordance with the ethical procedures of the Birmingham University Imaging Centre.

Stimuli and apparatus

Participants searched for a white uppercase T, which was presented 90° right or 90° left of vertical (randomly on each trial). Distracters were white uppercase L's presented at various orientations (0°, 90°, 180°, and 270°, see Fig. 1). All stimuli were formed from 2 equal length lines. Stimuli were presented on a black background with a central red fixation point (0.27° × 0.27°, at a distance of 65 cm). The experiment was created using Matlab (The Mathworks; Natick, MA) and the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997).

A circular virtual matrix composed of 6 concentric grids with radii of 1°, 2.1°, 3.2°, 4.9°, 7° and 9.1° provided 84 possible stimulus locations. Starting from the inner-most grid, there were 4, 8, 16, 12, 20 and 24 cells per grid and stimuli were presented in the centre of the cells. The stimuli presented were 0.63° × 0.63° on the three innermost circular grids and 1.37° × 1.37° on the outer grids (Dougherty et al., 2003; Horton and Hoyt, 1991). The display was divided vertically and horizontally, resulting in four display quadrants, each containing 21 possible stimulus locations. For each trial, stimuli were randomly assigned to the cells in either the lower-right or upper-left quadrant. This stimulus configuration exploits the retinotopic nature of the early visual cortex so that activation (and thus modulations of activation) to stimuli in the two quadrants is easily localised. Initial piloting suggested that some older adults may have trouble switching between four possible quadrants (likely due to the known age-related difficulty for task switching, e.g. Kray and Lindenberger, 2000) so the number of possible locations was reduced to two. We used opposite quadrants to reduce the possibility of participants simply moving their eyes towards the stimulus. There were two possible set sizes of 6 or 10 stimulus items.

Behavioural methods

Participants completed four experimental scans (each 8 min 50 s) with the exception of two older adults who, due to time

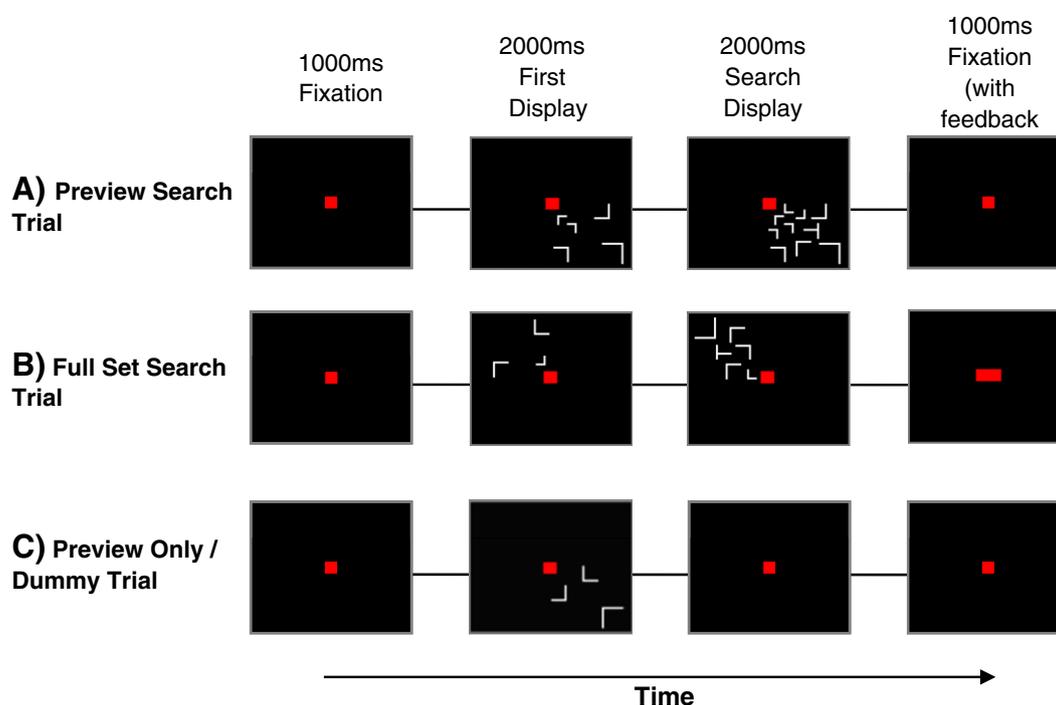


Fig. 1. Experimental procedure and stimuli. (A) A Preview Search trial with 10 search items. Half of the items (distracters) are presented in the first display for 2000 ms before being joined by the remainder of the distracters and the target (a T tilted \pm from vertical) for another 2000 ms in the search display. (B) A Full Set Search trial with 6 search items. Half of the items are presented in the first display but these are uninformative; these distracters offset at the start of the search display and are replaced with all the distracter items and the target within the same quadrant. Both trial types display a target item in the search display and the task is to decide the tilt direction of the target. The shape of the fixation square at the end of the trial provides feedback; it remains a square if the response is correct (A) and changes to a rectangle following an incorrect response (B). (C) A Preview Only/Dummy trial (type dependent on whether presented in the Preview or the Full block). No search display is presented during these trials, requiring no response. Participants were instructed to fixate on the fixation square throughout the experiment.

limitations, completed three scans. There were two blocks of trials per scan; a Preview block and a Full (baseline) block. In the Preview block there were two types of trials (see Figs. 1A and C). A Preview Search trial (12 per block) consisted of two consecutive two second displays. The first display, the preview display, presented half of the distracter items (either 3 or 5). The second display, the search display, presented the remaining items (either 2 or 4) plus the target amongst the previewed items in the same quadrant. The task was to decide the tilt direction (left or right) of the target, using a response box held in the right hand. No response or a response after the display was removed was counted as incorrect. A Preview Only trial (6 per block) consisted only of the preview display which was then followed by 2 s of fixation. Participants did not make a response to these trials. Although participants were aware that there would be Preview Only trials, they did not know when they would occur. Each trial began and ended with 1 s of fixation. Feedback was given via a shape change of the fixation square after search trials. Optseq2 (<http://surfer.nmr.mgh.harvard.edu/optseq>) was used to randomly select trial order and ITI length (between 4 and 12 s). For each unique combination of set size and quadrant there were 12 Preview Search trials and 6 Preview Only trials across all 4 scans.

During the Full block, there were two trial types; Full Set Search and Dummy (see Figs. 1B and C). In a Full Set Search trial, there were 3 or 5 distracters presented in the first display which disappeared at the onset of the search display. 5 or 9 new distracters plus the target were presented in the search display (in the same quadrant). Thus, the number of stimulus items in the second search display here was the same as in the search display of a Preview Search trial. The Dummy trials were identical to the Preview Only trials. Trial numbers, sequences, set sizes and presentation quadrants were identical to those in the Preview block.

Ordering of the two blocks within a scan was counterbalanced across participants and scans. The fixation square was present across the whole scan, with a period of 30 s of fixation at the beginning of each scan, a period of 31 s of fixation between the two blocks and at the end of each scan. Each block was preceded with a three second instruction screen. Participants were encouraged to keep fixating the square during the entire scan, using their peripheral vision to perform the task. They were informed an eye tracker would be monitoring their eye position. Participants were also instructed that it would be beneficial for them to attend and then ignore the previewed distracters in the first displays of the trials in the Preview block but that this strategy would not be useful in the Full block. Prior to the scanning session, each participant completed a practice session outside of the scanner. The practice consisted of two shorter runs of the experimental task without the Preview Only and Dummy trials. Two older adults required two practice sessions. Average correct performance on the practice session was 80.5% for the old adults and 85.5% for the young group. During practice, it was established that two older participants required 4 s search time to complete the task successfully. For these participants, search time (although not preview/first display time) in the scanning session was increased to 4 s.

Eye tracking

Eye position was continuously recorded using an ASL504 eye tracker. Any trials in which eye position exceeded 2.5° /visual angle from fixation, or where eye position data was lost for 150 ms or more were removed. Due to technical failure, eye tracking recording was not always successful and, where possible, the authors viewed the live display of participants' eyes on a monitor. Participants

remained fixated but occasional trials with gross eye movements were removed.

Quadrant mapping

A black-and-white contrast-reversing (8 Hz) checkerboard 90° wedge was used to locate the early visual areas that represent the four quadrants of the visual display for 8 younger and 16 older participants. The wedge appeared in a randomly selected quadrant for 4 s, and each quadrant was stimulated a total of 15 times interspersed with four second periods of fixation. There were 30 s of fixation at the start and the end of the scan. There was a small fixation cross in the centre of the screen. The task was to fixate on this whilst covertly attending to the wedge. The scan lasted 6 min. A design matrix was created with one regressor representing each quadrant, with each 4-second wedge duration modelled as a separate event. Each regressor was contrasted against baseline (fixation). The 6 movement parameters obtained during motion correction were added as regressors of no interest. Group analysis was conducted using FMRIB's Local Analysis of Mixed Effects (Beckman et al., 2003; Woolrich et al., 2004b). The purpose of analysis was to identify a peak of activation related to each quadrant of the visual field. To do this, Z (Gaussianised T/F) statistic images were first thresholded at $p < 0.05$ (uncorrected) and the peak activated voxel was identified for each quadrant. A spherical ROI with a radius of 4 mm was grown around each peak voxel, resulting in two ROIs corresponding to early visual cortex. These ROIs were found in the intracalcarine cortex, and were contralateral and inverted relative to the location of the wedge. This is consistent with the established retinotopic configuration of early visual cortex.

fMRI methods

A 3T Philips Achieva MRI scanner was used to acquire blood oxygenation level-dependent (BOLD) T2*-weighted echoplanar images for both quadrant mapping and the experimental scans. 30 ascending slices were acquired with a repetition time of 2000 ms, a time to echo of 35 ms, a flip angle of 85° and a resolution of 2.5 mm³. During the same session, a T1-weighted high resolution anatomical scan (1 mm³) was acquired. Participants laid supine within the scanner and a projector screen was viewed via a tilted mirror on the eight-channel SENSE head coil. If required, MR-compatible glasses were worn.

fMRI analysis

To process and analyse the MRI data, the fMRI Expert Analysis Tool (FEAT) Version 4.1.6 (part of FMRIB's Software Library, available at www.fmrib.ox.ac.uk/fsl) was used. Each functional scan was pre-processed, including head motion correction (absolute mean displacements averaged across search scans: Old = 0.39 mm; Young = 0.33 mm), slice-timing correction, non-brain removal, spatial smoothing (5 mm full-width at half maximum Gaussian kernel), intensity normalisation and high-pass Gaussian-weighted temporal filtering (search scans: sigma = 50 s; quadrant mapping scans: sigma = 30 s). The functional data sets from each participant were aligned to their anatomical image and transformed into Montreal Neurological Institute (MNI) space. To screen for unexpected artefacts in the data, Probabilistic Independent Component Analysis (Beckmann and Smith, 2004) implemented in MELODIC (Multivariate Exploratory Linear Decomposition into Independent Components), part of FMRIB's software library, was used. For each functional scan the components arising from MELODIC were assessed for artefacts, such as activation outside the head or from scanner artefacts, and any such components were removed. For the old participants, only 23 (of a total of 66) of the search scans required component removal.

Of these scans an average of 2.09% search scan components were removed. Similarly, for the young participants, only 6 (of a total of 60) of the search scans required component removal. Of these scans an average of 0.98% search scan components were removed.

For each scan, general linear modelling analysis was conducted using FILM with local auto-correlation correction (Woolrich et al., 2001). Each experimental condition was modelled as a separate regressor (convolved with a gamma function) according to the following factorial design: 4 (trial type: Preview Search, Preview Only, Full Set Search and Dummy) by 2 (quadrant: lower-right and upper-left). Set size was not included as a factor. Events in the Preview Search and Full Set Search trial regressors were defined as the duration from the onset of the first preview display to the response time. Events in the Preview Only and Dummy trial regressors were the duration of the first displays only. Trials with incorrect responses and trials identified as being non-fixated by eye tracking were modelled as regressors of no interest as were the 6 movement parameters obtained during motion correction. Contrasts of interest were first modelled within each scan and then were averaged across scans for each participant using fixed-effects analysis. Group analysis was conducted using FMRIB's Local Analysis of Mixed Effects (Beckman et al., 2003; Woolrich et al., 2004a). Z (Gaussianised T/F) statistic images were thresholded with an extent of $k > 50$ and a significance threshold of either $p = 0.05$ or $p = 0.01$ to ensure that all differences between age groups were documented. All group analyses were limited to grey matter. To interrogate regions-of-interest (ROIs), Featquery was used to establish mean percent signal change, and Perl Event-related Average Timecourse Extraction tool (<http://www.jonaskaplan.com/peate>) was used to extract time course data.

Psycho physiological interaction (PPI) analysis

To examine brain activity functionally connected to critical regions we conducted psycho physiological interaction (PPI) analyses. The voxel with the highest z-score from the source brain region was identified from the group analysis (i.e. precuneus, see below) and a 6 mm spherical ROI was centred on this voxel. The mean BOLD time courses were extracted from this source region for each of the participant's scans. An individual PPI analysis was conducted on each scan separately and included 8 regressors that represented the interaction between the time course of the source region and the 8 experimental conditions. Contrasts of interest included Preview Search–Full Search (and vice versa) and Preview Only–Dummy (and vice versa) for each quadrant. Data was averaged within each participant before being entered into a group-level analysis as above.

Results

Behavioural data

Reaction time and accuracy data from 32 participants were collapsed across the search scans.

Accuracy

Accuracy was high throughout the experiment. We calculated the proportion of correct responses for each search condition, set size and age group (Table 1). A repeated measures analysis of variance (ANOVA) with within-subjects factors of condition (Full Set Search,

Table 1
Proportion of correct responses for each search condition, set size and age group.

Set size	Full Set Search		Preview Search	
	Young	Old	Young	Old
6	.88	.83	.93	.89
10	.78	.72	.87	.79

Preview Search) and set size (6, 10 items) and a between-subjects factor of age (Young, Old) showed that accuracy was higher in Preview Search than in Full Set Search ($F(1,30) = 21.95$, $p = 0.00006$, partial $\eta^2 = 0.42$) and higher for 6 compared to 10 searched items ($F(1,30) = 39.04$, $p = 0.000007$, partial $\eta^2 = 0.57$). Accuracy was similar between age groups ($F(1,30) = 3.84$, $p = 0.06$, partial $\eta^2 = 0.11$) and there were no interactions between condition and age ($F(1,30) = 0.003$, $p = 0.96$, partial $\eta^2 = 0.00008$), set size and age ($F(1,30) = 0.52$, $p = 0.48$, partial $\eta^2 = 0.02$), set size and condition ($F(1,30) = 1.36$, $p = 0.25$, partial $\eta^2 = 0.04$), and condition, set size and age ($F(1,30) = 0.23$, $p = 0.64$, partial $\eta^2 = 0.01$). The significant effects of condition and of set size were not unexpected as the response deadline in the experiment will lead to very slow responses being recorded as errors. Consistent with this, RTs were longer and accuracy lower in both the Full Set Search condition and at the larger set size. This suggests that RTs were artificially curtailed by our fixed response time.

Reaction times

We used adjusted response time (RT_{adj}) instead of RT as the dependent measure to account for the restricted response period. We divided the average correct RT (excluding incorrect responses and timed out responses) for each participant, condition and set size combination by the proportion correct for that combination. Given that the discrimination between the two targets can be expected to be perfect given sufficient time (they are easily discriminable, even in the periphery) we assumed that the majority of errors reflected participants responding before they correctly found the target. The adjusted response time slightly and proportionately increased the estimated reaction time (see also Payne and Allen, 2011). Fig. 2 plots the RT_{adj} against set size for the Full Set Search and Preview Search conditions for each age group separately.

RT_{adj} data for the correct trials were entered into a repeated measures ANOVA with within-subjects factors of condition (Preview Search, Full Set Search) and set size (6, 10 items), and a between-subjects factor of age (Young, Old). Participants responded quicker in the Preview Search condition ($F(1,30) = 48.269$, $p = 0.0000001$, partial $\eta^2 = 0.617$) and at the smaller set size ($F(1,30) = 44.58$, $p = 0.0000002$, partial $\eta^2 = 0.598$). Older adults were slower than younger adults ($F(1,30) = 13.449$, $p = 0.001$, partial $\eta^2 = 0.31$). There were no significant differences between conditions or set sizes that were dependent on age group (condition \times age: $p = 0.739$; set size \times age: $p = 0.085$). Participants displayed a standard preview benefit (Watson and Humphreys, 1997) that is, there was an improvement of search efficiency (in terms of time per item) in the Preview Search condition compared to the Full Set Search condition (interaction of condition and set size: $F(1,30) = 7.171$, $p = 0.012$, partial $\eta^2 = 0.193$). Older and younger adults both benefited from

previewing the distracters in the Preview Search condition (no interaction of condition, set size and age: $p = 0.516$).

Inspection of individual participants' data revealed that some participants (in both groups) did not benefit from the preview display. 10 of the 17 old adults and 12 of the 15 young adults were categorised as "Previewers". The remaining participants were "Non-Previewers" defined as those who had no efficiency gain, in terms of slope for Preview Search, compared to the Full Set Search condition. Confirming this categorisation, an ANOVA with condition (Full Set Search, Preview Search), age group (Young, Old), set size (6, 10 items) and preview status (Previewer, Non-Previewer) revealed a 3-way interaction between condition, set size and preview status: ($F(1,28) = 24.969$, $p = 0.00003$, partial $\eta^2 = 0.471$), see Figs. 3A and B. Analysing the Previewers alone produced similar results to the overall analysis above, with main effects of condition ($F(1,20) = 52.328$, $p = 0.0000005$, partial $\eta^2 = 0.723$), set size ($F(1,20) = 48.298$, $p = 0.000001$, partial $\eta^2 = 0.707$), age group ($F(1,20) = 9.599$, $p = 0.006$, partial $\eta^2 = 0.324$), and the standard preview benefit interaction of condition \times set size ($F(1,20) = 31.427$, $p = 0.00002$, partial $\eta^2 = 0.611$). Analysing the non-previewers alone showed that they were also slower for larger, compared to smaller set sizes ($F(1,8) = 5.629$, $p = 0.045$, partial $\eta^2 = 0.413$). There was also an interaction between condition and set size ($F(1,8) = 8.583$, $p = 0.019$, partial $\eta^2 = 0.518$) but inspection of Fig. 3 shows that non-previewers were actually less efficient (in terms of slope) for Preview Search compared to Full Set Search. Inspection of Fig. 3 also shows that in all cases (overall, lower-right, upper-left) slopes in the preview condition are steeper for non-previewers than previewers. We were interested in whether, if older adults are able to preview, they use the same underlying processes as younger people who preview, and thus initially we restricted our analysis to the previewers in each age group. Later, to verify that patterns in our data are attributable to task based differences, we compared between previewers and non-previewers.

We also investigated whether benefiting from the preview display requires modulation of early visual areas. For instance, does visual activation have to change compared to baseline for a preview benefit to occur, irrespective of any top-down signalling (or absence of it)? For this, we needed a tighter link between behaviour and brain activity. We cannot know whether participants are excluding the preview on a trial by trial basis (or even over a few trials) because the preview benefit emerges as a slope change over a series of trials. Instead we averaged trials from the lower-right (LR) and upper-left (UL) quadrants separately. When the stimulus was presented in the LR quadrant 7 older adults and 11 younger adults benefited from the preview display. When the stimulus was presented in the UL display 10 older adults and 10 younger adults benefited from the preview display. For previewing participants, Preview Search was faster than Full Set Search (LR: $F(1,16) = 26.857$, $p = 0.00009$, partial $\eta^2 = 0.627$, UL: $F(1,18) = 17.966$, $p = 0.0005$, partial $\eta^2 = 0.5$), a smaller number of distracters led to shorter reaction times

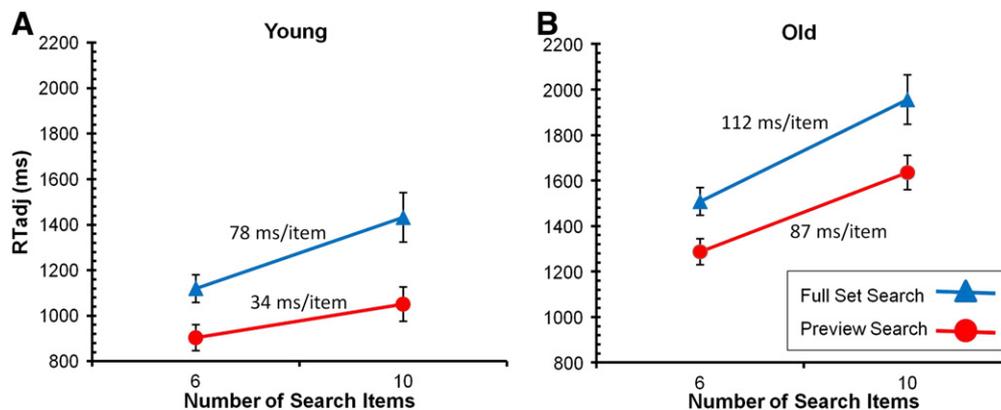


Fig. 2. RT_{adj} (see text for definition) for young (A) and old (B) participants performing Full Set Search (triangles) and Preview Search (circles) in the scanner. Vertical bars represent ± 1 Standard Error. Text on plot is time per item for each condition.

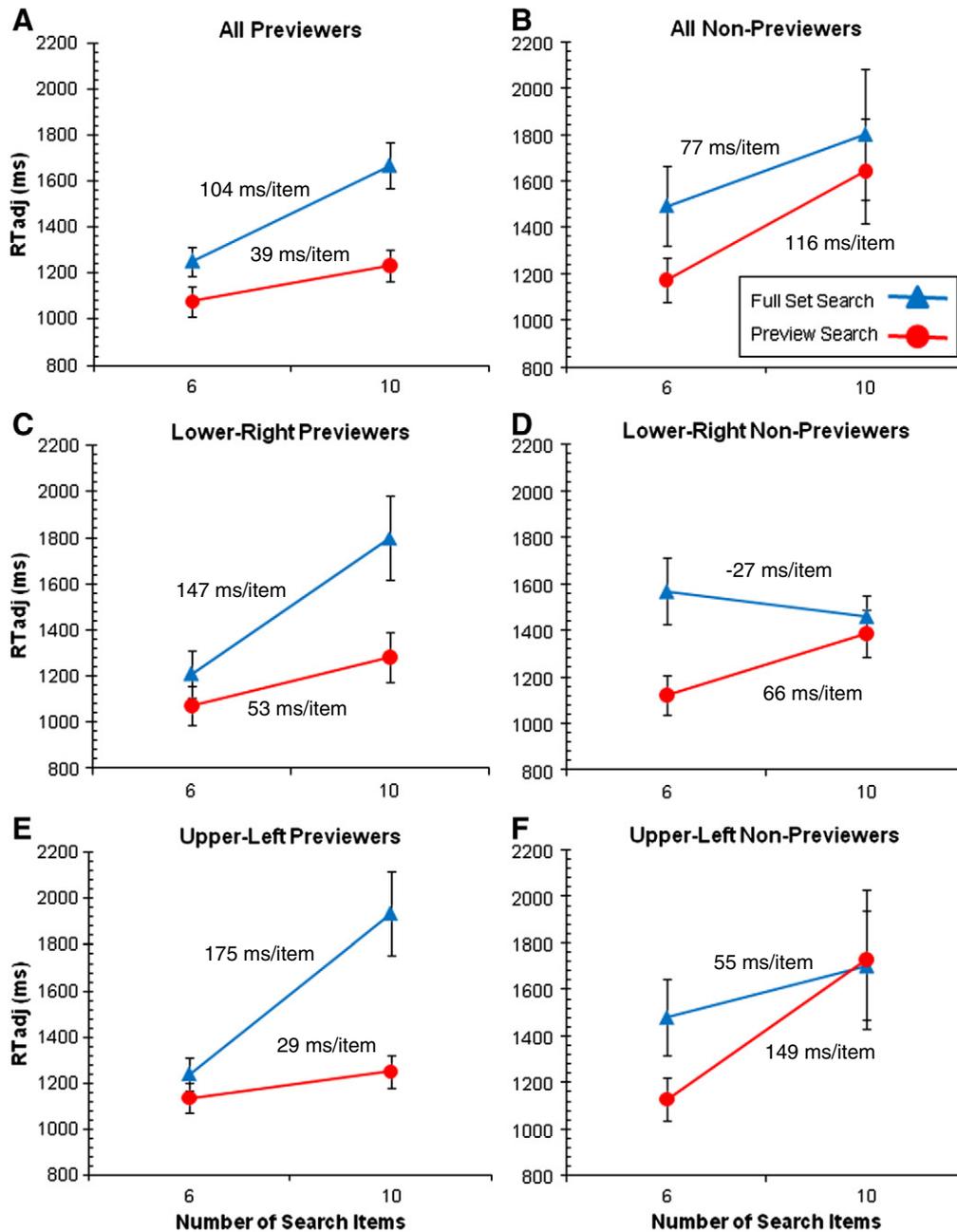


Fig. 3. Preview Search (circles) and Full Set Search (triangles) performance in terms of RT(adj) for each set size, grouped depending on whether the participants were able to use the preview display to improve performance (see text). A and B: participant data split into those that preview and those that do not preview. C–F: data is split by previewing status dependent on the stimulus location, which was either in the lower-right (LR) or upper-left (UL). Vertical bars represent ± 1 Standard Error. Text on plot is time per item for each condition.

(LR: $F(1,16) = 42.61$, $p = 0.000007$, partial $\eta^2 = 0.727$; UL: $F(1,18) = 18.007$, $p = 0.0005$, partial $\eta^2 = 0.5$) and search was quicker for the larger set size in the Preview Search condition only, indicating a benefit from preview (LR: $F(1,16) = 33.492$, $p = 0.00003$, partial $\eta^2 = 0.677$, UL: $F(1,18) = 13.924$, $p = 0.002$, partial $\eta^2 = 0.436$), see Figs. 3C–F. There was one difference between the quadrants which was that older adults were slower than young adults for stimuli in the LR quadrant ($F(1,16) = 8.658$, $p = 0.01$, partial $\eta^2 = 0.351$) but this did not interact with condition or set size, or both. For the non-previewers, the interaction between the number of items and the condition was either non significant (UL, $p > 0.5$) or significant but in the opposite direction (Old non-previewers only, LR: $F(1,9) = 7.31$, $p = 0.024$, partial $\eta^2 = 0.448$). We used these differences in ability to benefit from the preview between participants as a variable in our fMRI analyses to search

for BOLD activation that was specifically linked to being able to exclude the previewed items. This enabled us to find the neural signature related to successful previewing whilst removing noise associated with merely searching the stimulus display.

Imaging data

Preview-related neural activity: separate age groups

First, we identified brain areas showing preview-related activity in participants who were able to use the preview ('Previewers') for the two age groups separately. For each age group, we contrasted Preview Search trials against Full Set Search trials. Consistent with previous findings, we found activation in the precuneus relating to ignoring the preview display for both younger and older age groups.

Table 2

Regions where young, or old, adults showed higher activity in Preview Search than the Full Set Search baseline.

	Structure	Co-ordinate (mm)	Z score	Extent (voxels)
Young	L Juxtapositional Lobule	-2 -12 64	3.27	404
	L Lateral Occipital Cortex	-50 -64 38	3.09	313
	R Lateral Occipital Cortex	52 -62 20	3.08	204
	L Precuneus	-2 -60 40	3.06	157
	R Superior Frontal Gyrus	0 52 46	3.25	141
	L Middle Frontal Gyrus	-36 18 54	2.93	108
	L Superior Parietal Lobule	-46 -44 58	2.75	58
Old	L Precuneus	-6 -50 52	2.99	98
	R Postcentral	56 -22 50	2.91	52

Additionally, younger adults invoked extra areas during previewing including frontal and occipital regions (see Table 2 and Fig. 4).

Preview-related neural activity: comparing age groups

To find differences in activation patterns between the age groups we contrasted Preview Search trials against Full Set Search trials (as above) and then contrasted these between the two age groups (see Table 3 and Fig. 5). Despite overlap between the activation patterns in the two age groups there were also considerable areas of difference. For instance, for the younger adults, there was higher activity in several frontal regions and the precuneus. For the older adults there was greater activity in occipital and parietal lobes.

We extracted mean percent signal change from the activated clusters larger than 100 voxels for each old versus young comparison (from Table 3). Fig. 6 shows the average change in activation (compared to fixation) for the three largest clusters for each comparison and plots for the remainder can be found in the supplementary information. Supplementary Table 1 shows the correlations between participants benefit from preview and the change in activation between the conditions. It is clear that the pattern of activation between the conditions and between age groups varied from region to region. We carried out separate ANOVAs on the percent signal change from each region with condition (Preview Search, Full Set Search) and age group (Young, Old) as variables. As expected based on how the regions were defined, for most of the regions (Left Precentral, Left Occipital cortex, Right Central Operculum, Left Superior Parietal Lobule, Left Lingual Gyrus (borderline)) activity was higher for older, compared to younger participants (PreC: $F(1,20)=6.252$ $p=0.021$ partial $\eta^2=0.24$, Occip: $F(1,20)=7.99$ $p=0.01$ partial $\eta^2=0.286$, Operc: $F(1,20)=17.132$ $p=0.001$ partial $\eta^2=0.461$, LSPL: $F(1,20)=5.953$ $p=0.0024$ partial $\eta^2=0.229$, LLing: $F(1,20)=4.255$ $p=0.052$ partial $\eta^2=0.175$). Importantly, in each of these regions the pattern of activity was different for younger, compared to older participants. Activity for the Preview Search condition was higher than for the Full Set Search condition for the old participants but the opposite was

Table 3

Regions where preview-related activity between the age groups differed. Top: areas where the activation for Preview Search (compared to Full Set Search) was higher for old than young adults. Bottom: the same but for young greater than old adults.

Comparison	Structure	Co-ordinate (mm)	Z Score	Extent (voxels)	
Old > Young	L Precentral Gyrus	-60 2 8	2.71	313	
	L Occipital Pole	-10 -98 20	2.62	283	
	R Central Opercular Cortex	46 -14 26	2.73	156	
	R Occipital Pole	16 -96 22	2.23	142	
	L Superior Parietal Lobule	-22 -54 44	2.66	138	
	L Lingual Gyrus	-20 -68 -6	2.69	127	
	R Superior Temporal Gyrus	46 -36 4	2.42	112	
	R Middle Frontal Gyrus	36 30 32	2.41	92	
	L Inferior Frontal Gyrus	-32 30 14	2.45	81	
	R Parietal Operculum Cortex	44 -36 24	2.26	58	
	R Precentral Gyrus	36 6 32	2.05	53	
	Young > Old	L Precuneus	-2 -60 38	2.57	632
		R Superior Frontal Gyrus	0 52 44	2.84	465
L Lateral Occipital Cortex		-34 -68 56	2.85	428	
R Lateral Occipital Cortex		54 -64 18	2.7	228	
L Middle Frontal Gyrus		-40 10 46	2.28	116	
L Superior Frontal Gyrus		-22 22 38	2.57	73	
R Paracingulate Gyrus		2 50 18	2.4	69	
R Superior Frontal Gyrus		22 34 52	2.57	65	
L Precuneus		-2 -76 50	2.3	65	
R Superior Frontal Gyrus		6 30 56	2.57	52	

true for the young participants (PreC: $F(1,20)=8.65$ $p=0.008$ partial $\eta^2=0.3$, Occip: $F(1,20)=12.252$ $p=0.002$ partial $\eta^2=0.38$, Operc: $F(1,20)=4.894$ $p=0.039$ partial $\eta^2=0.197$, LSPL: $F(1,20)=12.679$ $p=0.002$ partial $\eta^2=3.888$, LLing: $F(1,20)=6.885$ $p=0.016$ partial $\eta^2=0.256$). A similar pattern was found in the precuneus but in addition, activity for Preview Search was higher than that for Full Set Search overall (Preview > Full Set: $F(1,20)=15.481$, $p=0.001$ partial $\eta^2=0.436$, Old > Young: $F(1,20)=15.605$ $p=0.001$ partial $\eta^2=0.438$, Condition \times age: $F(1,20)=6.638$ $p=0.018$ partial $\eta^2=0.249$). The interaction of age and condition was also found in the Left Superior Temporal Gyrus although without the main effect of age or condition (LSTG: $F(1,20)=6.497$ $p=0.0019$ partial $\eta^2=0.267$). The opposite interaction, with higher activation for Full set than preview for the old participants but the opposite effect for the young was found in the Right Lateral Occipital cortex ($F(1,20)=7.3$ $p=0.014$ partial $\eta^2=0.267$). Activity in the right superior frontal gyrus was higher for old than young participants in all conditions ($F(1,20)=8.615$ $p=0.008$ partial $\eta^2=0.301$) but there was no interaction between the conditions. Finally, the Left Lateral Occipital and left Medial Frontal Gyrus cluster showed no significant effects or interactions in this analysis.

It seems, therefore, that to maintain the same behavioural performance old and young adults had different profiles of activation. For old adults, successfully benefiting from preview is related to increases

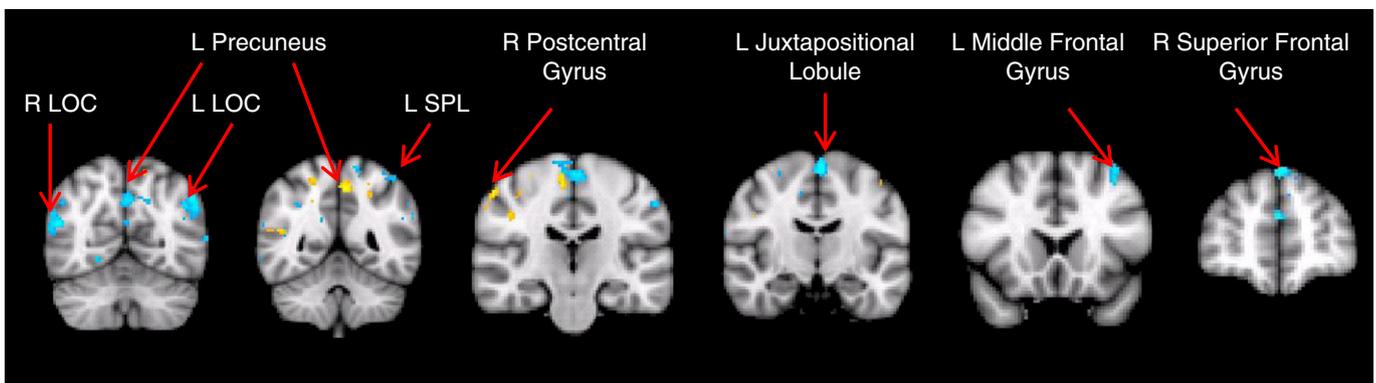


Fig. 4. Areas which show activation for old (yellow) and young (blue) participants in Preview Search compared to Full Set Search (see Table 2).

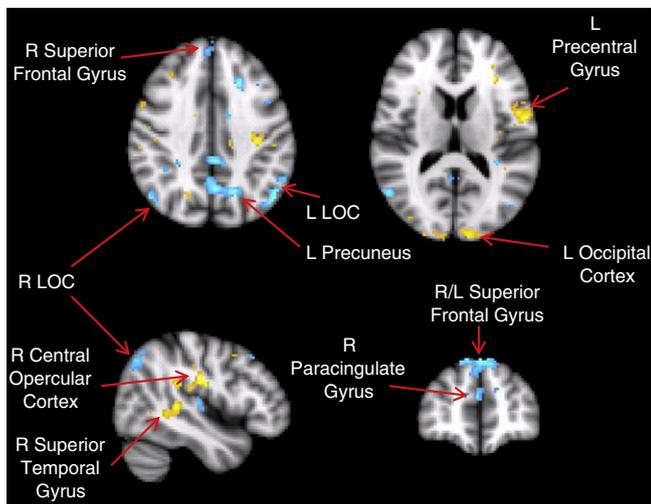


Fig. 5. Areas which show a difference between old and young participants in Preview Search compared to Full Set Search (see Table 3). Yellow: Old adults > young adults. Blue: Young adults > old adults.

in activity, both overall and compared to Full Set Search in relatively posterior regions. Note that all these regions also showed a weak but consistent negative correlation between behaviour and benefit from preview for older, but not younger, adults (Supplementary Table 1, top part) suggesting that greater activation in the preview condition led to greater improvements in performance. For younger adults, on the other hand, successful preview search was linked to lower activation.

Furthermore, in the precuneus, a region found to be critical to this task, both age groups showed higher activity in the preview condition. For young adults, however, there was a reduction in suppression of this region rather than an increase in positive activation for preview search.

To confirm that these effects were task specific, we extracted the activation from the same areas from the participants who did not preview. In the Left and Right Occipital Lobe, left PreCentral Gyrus, Medial Frontal Gyrus, Precuneus, SPL, Lingual Gyrus, Superior Temporal Gyrus and right LOC there were no significant effects of age or condition, nor were there significant interactions between these variables ($p > 0.2$). Activation was significantly higher for older adults than younger adults in the Operculum ($F(1,8) = 8.955$, $p = 0.017$, $\eta^2 = 0.528$) and there was a similar trend in the Superior Frontal Gyrus ($F(1,8) = 3.716$, $p = 0.09$, $\eta^2 = 0.317$). In the left LOC there was a borderline increase in activation for the Full Set Search condition compared to Preview Search ($F(1,8) = 3.915$, $p = 0.083$, $\eta^2 = 0.329$) but this did not interact with task or age. Thus, the differential activation of these regions by task and age was specific to participants who were able to exclude the previewed items. For comparison, Supplementary Fig. 2 shows BOLD activation for older non-previewer adults (there were only 3 non-previewer young adults). The next stage of the analysis looked in more detail at the earliest visual areas.

Early visual cortical activation

Investigating preview-related activations for the early visual regions is complicated by the stimulus difference between the conditions. It is a necessary part of the design that there are more new items appearing in the second display of Full Set Search than in Preview Search. In addition, the main task and response were in the second, to-be-searched display of each trial. The preceding analysis covering the whole trial period is likely to be mostly influenced by the activations during the second display. In each condition, however, on a minority of trials, we presented only the first display

(the Preview Only and the Dummy trials). The stimulus on these trials is exactly the same in Preview Search and Full Set Search conditions. Participants did not know when these trials would appear and thus the only difference between these trials is the participants' expectation. Thus we can measure activity in each condition without the confounding factor of the new onsets, which is particularly important when comparing activity in the early visual areas.

It is also important to separate activity relating to successful preview trials from trials where, whatever the intent, the participant did not benefit from preview. The imaging data was analysed separately for each quadrant using only the previewing participants for that quadrant. Using the retinotopic mapping data, we identified the early visual areas responding to the LR and UL quadrants and extracted the timecourse data of the LR and UL Dummy and Preview Only trials from these V1 regions of interest (ROI), see Fig. 7.

Activity increases on presentation of the stimulus in all conditions. To investigate the differences between groups and conditions for the UL quadrant we carried out a repeated measures ANOVA with within-subjects factors of condition (Preview Only, Dummy) and time (5, 6, 7, 8, 9 s from onset of first display), and a between-subjects factors of age (Young, Old). Activity changed significantly with time ($F(1.304, 23.465) = 6.571$, $p = 0.012$, $\eta^2 = 0.267$) but this was moderated by the condition ($F(2.012, 36.217) = 4.532$, $p = 0.017$, $\eta^2 = 0.201$). The change in activation for the conditions was moderated by age group ($F(1, 18) = 4.754$, $p = 0.043$, $\eta^2 = 0.209$). Thus, there were differences between conditions depending on age group and time. To explore the interaction between condition and age, separate ANOVAs were performed on the two age groups. There was a significant interaction between condition and time for the older age group ($F(1.897, 17.074) = 4.864$, $p = 0.023$, $\eta^2 = 0.351$) but no significant effects for the younger age group. For the older age group, the Preview Only condition is significantly more activated in V1 than the Dummy condition, but this is not the case for the younger age group. A whole head GLM analysis comparing Preview Only to Dummy trials confirmed greater activation for the older relative to the younger adults in the right ventral occipital cortex (12, -92, -8), a similar location to the retinotopically mapped right hemisphere ventral V1 (6, -86, -4). For participants who did not successfully use the preview, there was a significant increase in signal over time ($F(1.67, 16.696) = 7.382$, $p = 0.007$, $\eta^2 = 0.425$) but no further significant effects or interactions, confirming that the differences observed were due to the task.

In the LR ROI (using the same analysis as above) activity changed significantly over time ($F(1.687, 26.988) = 12.403$, $p = 0.0003$, $\eta^2 = 0.437$) and this was moderated by age ($F(1.687, 26.988) = 3.807$, $p = 0.041$, $\eta^2 = 0.192$). Fig. 7 (lower) shows earlier activity for older adults but no significant difference between activations for the two conditions. For participants who did not preview, there was a significant effect of time ($F(1.346, 16.152) = 6.565$, $p = 0.015$, partial $\eta^2 = 0.354$) but no interaction with condition or age. It is also not clear why differential activity should be seen in one visual field quadrant and not the other. It should be noted, however, that data was considerably noisier in the lower right quadrant and for some participants the display was partially obscured by their optical correction goggles.

Connectivity analysis

Whilst both old and young adults are able to benefit from preview, the pattern of brain activity underlying this appears different between young and old adults. We investigated the functional connectivity underlying performance. The precuneus showed activation for both old and young adults and has been found to be consistently active in previous investigations of the preview benefit so this was selected as the source of the connectivity. Exact selection of the source is important. The exact peaks of precuneus activity differed between

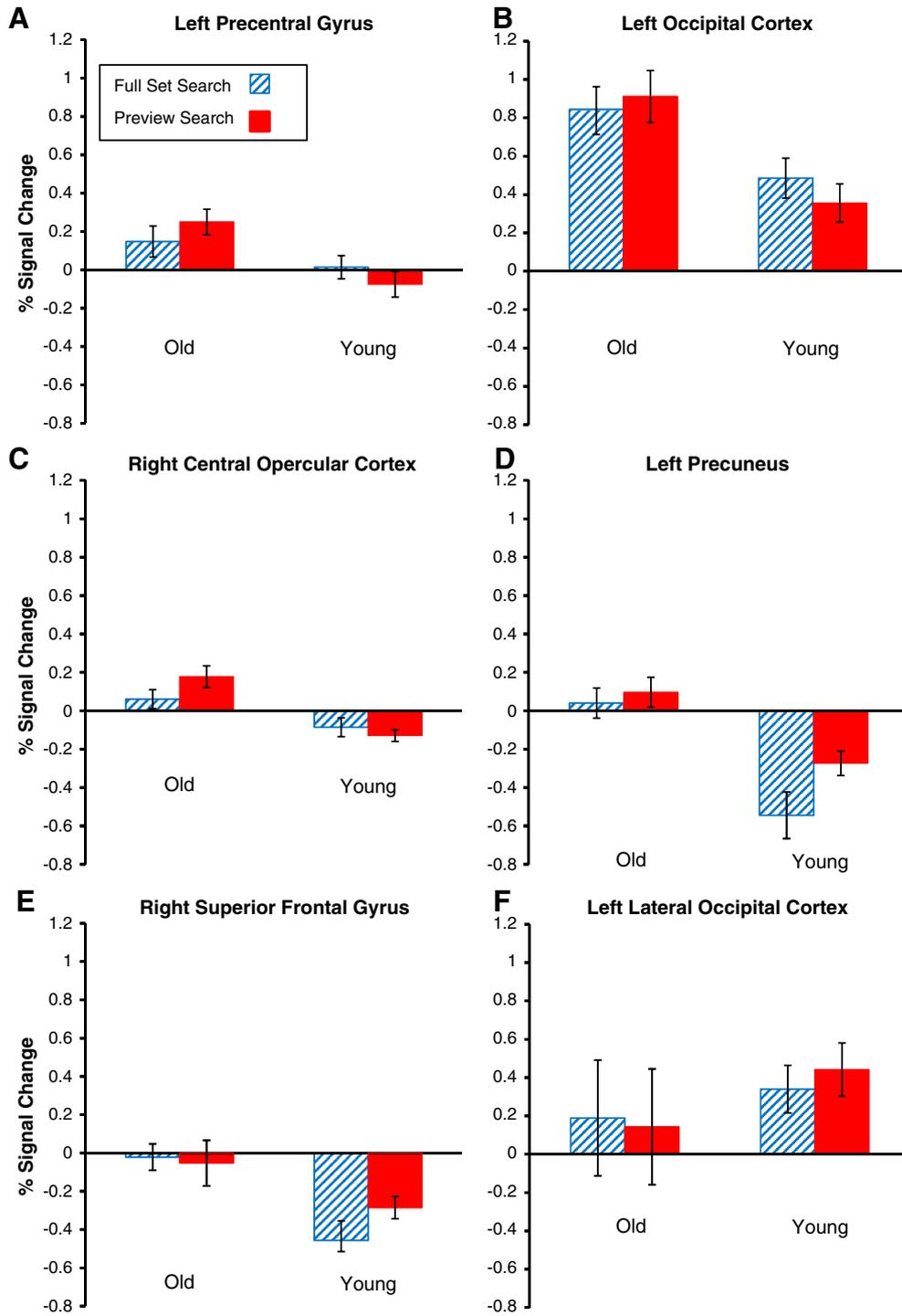


Fig. 6. Percent signal change for the 6 regions showing strongest differences between old and young adults when comparing Preview Search against Full Set Search. Signal changes were extracted from each quadrant for each scan individually and averaged within each participant, then averaged across the quadrants, and then averaged over the group. Vertical bars represent ± 1 Standard Error.

old and young adults and one option would have been to select different sources for old and young connectivity analyses. This is problematic as if different sources are used it would be difficult to interpret whether any differences in connectivity were due to differences in processes between young and old adults or difference between the sources. Thus we used the same source for both old and young adults. This was derived from an analysis of all previewing participants combined using the comparison of Preview Search and Full Set Search trials. Connectivity from this source was analysed for both the first display only trials (i.e. Preview Only > Dummy Only) and the search

trials (i.e. Preview Search > Full Set Search). Table 4 and Fig. 8 show regions that were significantly connected to this source region. There was more connectivity in the Preview Search trials than the Full Set Search trials for both older and younger adults in both anterior and posterior regions but the pattern of connectivity was different between the age groups. When analysing just the first display trials, there is more connectivity for older adults in the Preview Only trials (than the Dummy trials) towards parietal and frontal regions whereas younger adults have stronger connectivity to parietal and visual regions.

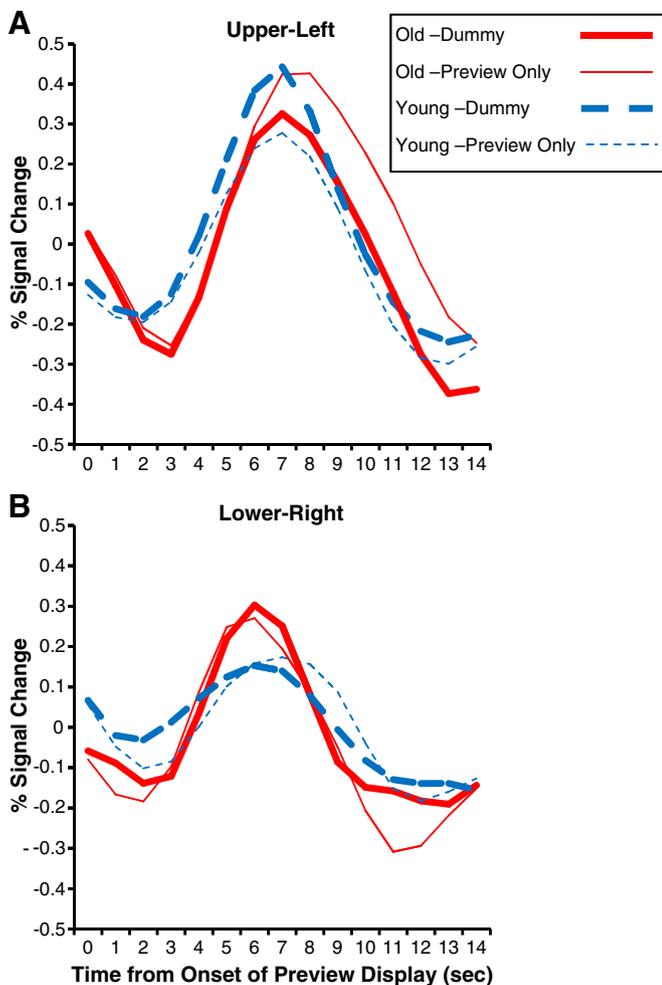


Fig. 7. The time course of activation for the upper-left V1 ROI (A) and lower-right V1 ROI (B) from the trials where only the first display was shown. Trials were embedded in either the Preview Search condition (Preview Only trials) or the Full Set Search condition (Dummy trials). Data is shown for the participants who benefited from the preview. The presentation time of the first display is at time 0. Data represent Dummy trials for old (thick solid line) and young participants (thick dashed line), and Preview Only trials for old (thin solid line) and young participants (thin dashed line).

Discussion

We found that for many older adults, the ability to exclude or ignore some items from search was preserved. Older adults who appeared to match younger adults' performance showed different patterns of underlying brain activity. We found overlapping activity for older and younger adults in regions previously shown to be critical for temporal segmentation (Dent et al., 2011), however, brain activity in other regions seldom overlapped. Even if the same areas were involved for the two age groups, patterns of activation differed between the groups and functional connectivity from the critical precuneus regions was not the same between the groups.

During the first display (Preview Only or Dummy), unlike Allen et al. (2008), Dent et al. (2011) and Payne and Allen (2011), for young participants there was no change in activation for the preview display compared to the Dummy trials. Older adults on the other hand, showed increased activation in visually responsive regions. The lack of early modulation for young adults could be due to a number of reasons. It is possible that active suppression is not required for this task, or that it is present but not detected by our analysis. It is possible that the suppression required to exclude the distracters used here is enacted elsewhere in the visual cortex. Fig. 6 shows lower activation for Preview Search, compared to Full Set Search in the left occipital cortex for

Table 4

Areas with significant connectivity to the precuneus in the older and younger adults for the contrast between Preview Search and Full Set Search trials, and Preview Only and Dummy trials ($p = 0.05$, $k > 50$).

	Structure	Co-ord (mm)	Z Score	Extent (voxels)	
<i>Preview Search > Full Set Search</i>					
Old	R Precuneus	8 -56 46	2.96	600	
	R Inferior Frontal Gyrus	44 8 16	2.72	599	
	L Parietal Operculum Cortex	-48 -32 20	2.4	275	
	L Inferior Frontal Gyrus	-40 16 24	2.57	239	
	R Lingual Gyrus	16 -48 -4	2.71	194	
	R Lateral Occipital Cortex	44 -70 22	2.59	167	
	L Angular Gyrus	-54 -52 12	2.47	128	
	R Lingual Gyrus	32 -50 -2	2.51	121	
	R Frontal Pole	16 36 38	2.45	66	
	L Lingual Gyrus	-24 -52 -2	2.28	64	
	L Superior Frontal Gyrus	-20 18 52	2.16	61	
	R Precentral Gyrus	60 12 24	2.66	56	
	L Insular Cortex	-36 -22 14	2.19	54	
	Young	R Precuneus	6 -76 40	2.4	330
R Angular Gyrus		56 -52 38	2.49	217	
R Paracingulate Gyrus		8 22 40	2.53	167	
R Precentral Gyrus		8 -22 64	2.68	155	
L Postcentral Gyrus		-42 -26 46	2.11	109	
R Postcentral Gyrus		36 -22 42	2.39	81	
R Lingual Gyrus		2 -90 -6	2.45	79	
L Lateral Occipital Cortex		-22 -86 36	2.21	76	
R Occipital Pole		16 -104 -6	2.61	76	
No label		22 -30 42	2.33	72	
L Cingulate Gyrus		-6 16 38	2.53	64	
R Middle Frontal Gyrus		40 4 60	2.17	53	
R Middle Frontal Gyrus		34 16 58	2.63	52	
R Precentral Gyrus		52 4 30	2.34	50	
Old > Young	L Angular Gyrus	-54 -52 12	2.77	562	
	R Precentral Gyrus	48 6 10	2.45	309	
	R LOC	44 -70 24	2.81	239	
	L Inferior Frontal Gyrus	-42 8 26	2.6	171	
	R Frontal Pole	16 36 32	2.38	117	
	R Superior Frontal Gyrus	4 54 38	2.17	87	
	R Precuneus	6 -58 46	2.4	84	
	L Cingulate Gyrus	-10 -44 34	2.43	71	
	R Lingual Gyrus	10 -52 -8	2.33	63	
	L LOC	-46 -66 20	2.16	62	
	R Occipital Fusiform Gyrus	24 -66 -8	2.38	55	
	Young > Old	L Cuneal Cortex	-10 -78 20	2.81	542
		R Supramarginal Gyrus	44 -30 38	2.74	332
		R Cuneal Cortex	8 -78 38	2.6	167
L Precentral Gyrus		-24 -26 66	2.43	141	
R Precentral Gyrus		6 -20 64	2.3	101	
L Precentral Gyrus		-12 -28 50	2.17	79	
R Cingulate Gyrus		10 14 36	2.3	78	
L Angular Gyrus		-32 -60 22	2.34	62	
R Superior Frontal Gyrus		8 22 64	2.43	53	
L Cingulate Gyrus		-10 10 32	2.34	53	
<i>Preview Only > Dummy</i>					
Old		L Supramarginal Gyrus	-42 -48 18	2.88	209
		L Supramarginal Gyrus	-48 -34 38	2.36	79
		L Precuneus	-4 -48 44	2.15	62
Young	R Precentral Gyrus	52 -10 44	2.54	430	
	R Postcentral Gyrus	48 -32 54	2.57	115	
	R Precentral Gyrus	8 -18 56	3.02	107	
	R Cingulate Gyrus	10 -44 28	2.4	106	
	R Superior Temporal Gyrus	64 -34 16	2.75	106	
	L Juxtapositional Lobule Cortex	-12 -14 52	2.43	86	
Old > Young	L LOC	-34 -76 -2	2.5	53	
	L Angular Gyrus	-38 -56 18	2.42	164	
Young > Old	L Frontal Pole	-22 50 20	2.28	115	
	L Supramarginal Gyrus	-60 -50 20	2.75	81	
	R Precuneus	20 -64 38	2.52	278	
	L Juxtapositional Lobule Cortex	-12 -14 50	2.74	243	
	R Postcentral Gyrus	50 -14 42	2.5	202	
	R Superior Temporal Gyrus	64 -32 14	2.6	138	
	R Postcentral Gyrus	60 -16 50	2.2	116	
	L Precentral Gyrus	-40 -10 46	2.21	109	
	L LOC	-36 -74 -4	2.29	94	
	L LOC	-38 -68 52	2.29	75	
	R Superior Parietal Lobule	38 -50 46	2.16	70	

Table 4 (continued)

Structure	Co-ord (mm)	Z Score	Extent (voxels)
R Cingulate Gyrus	4 -2 46	2.25	67
L Cingulate Gyrus	-8 -6 38	2.38	66
R Precentral Gyrus	38 8 28	2.07	57
L Occipital Pole	-10 -94 4	2.22	56

younger adults, for example. What is clear, however, from our results is that older adults are also not suppressing visual input for the preview, in fact, in some circumstances, for older adults, activation increases in the preview display.

Differential brain activation patterns in older and younger adults despite similar behavioural performance have been found in other tasks. Previous studies have tended to involve recruitment of additional regions rather than differential connectivity or activation patterns within multiple regions. Madden and colleagues (Madden,

2007), for example, have proposed that older adults maintain performance on attention based tasks by recruiting increasing amounts of the fronto-parietal attention network. In a visual search task, for instance older adults had higher activation in the frontal eye fields, middle frontal gyrus, supramarginal gyrus, angular gyrus and superior parietal lobe (Madden et al., 2007b). Younger adults, on the other hand had higher activation in the visual lobe. Furthermore, whilst for younger adults performance correlated with activation level in relatively posterior visual regions, for older adults performance only correlated with activation levels in the frontal eye fields (implicated in covert attention as well as eye movements). It was proposed that age-related declines in capacity or performance in the posterior sensory regions are compensated by increases in frontal, attention related regions. Consistent with this, we saw more connectivity to frontal regions for older adults during both the first (Preview) display and the analysis of the full length trials. It is during the first display that processes specific to temporal segmentation take place. These

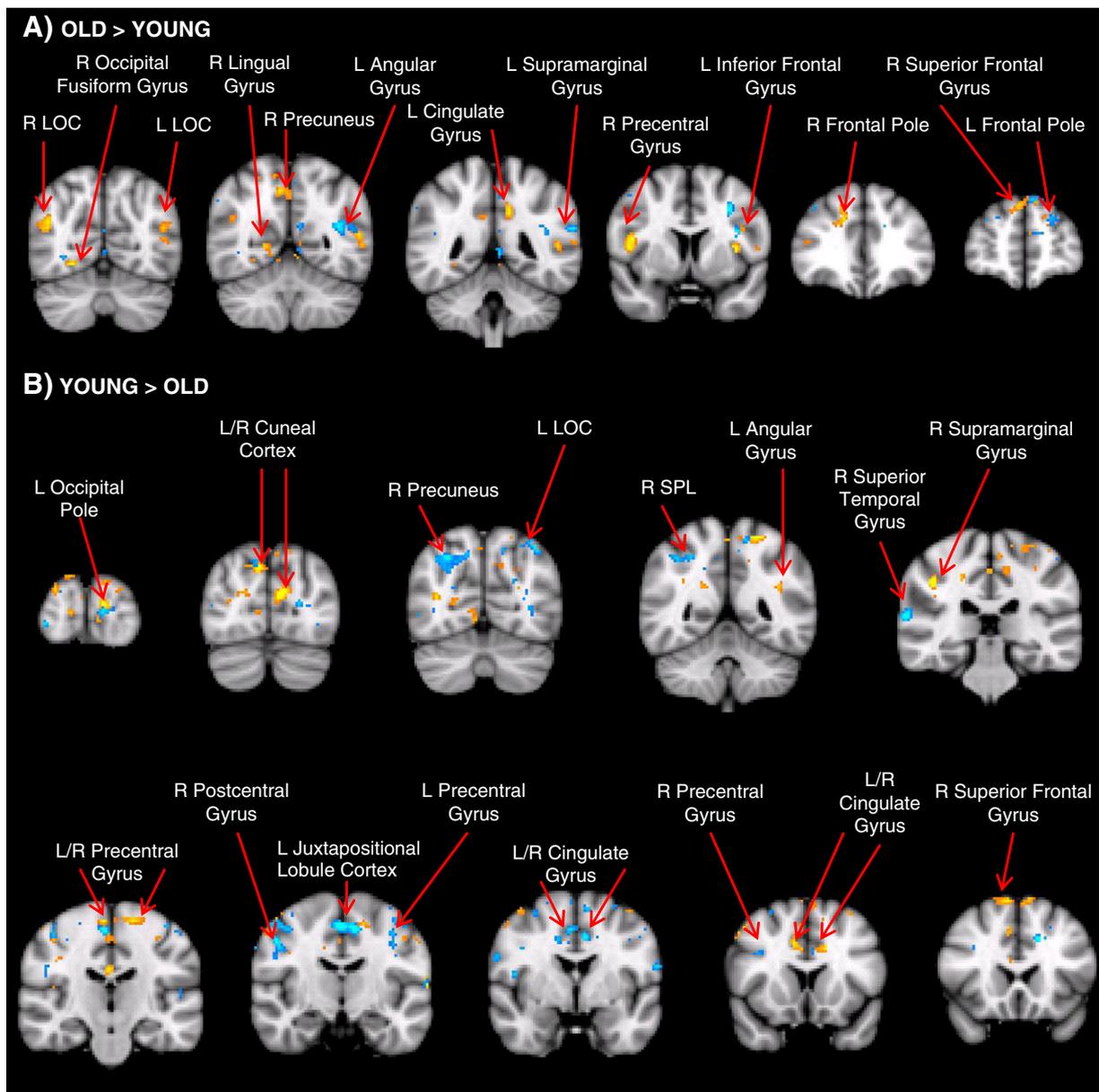


Fig. 8. Areas showing significant connectivity to the precuneus in the PPI analysis. A) Old > Young. B) Young > Old. Yellow shows areas where connectivity in the full length Preview trial is greater than in the full set trials. Blue shows similar but for the first display only trials (i.e. Preview Only > Dummy).

additional connections may be required to compensate for age-related losses in the ability to segment or suppress the distracters. We show that additional connectivity, without additional BOLD activations can lead to matched performance between older and younger adults. Over the whole length trials there was connectivity to frontal and parietal regions for both age groups. Frontal connections were more widespread for older adults however, consistent with their input being required to initiate compensation. BOLD activation levels, however, were higher in posterior regions, not frontal regions, for older adults; opposite to the predictions of compensation hypotheses.

Other theories describing the ageing brain suggest that there is increased activation in older, compared to younger, brains. The HAROLD theory of ageing (Cabeza et al., 2002, 2004) suggests that whilst activation in younger adults tends to be unilateral, activation in older adults tends to be bi-lateral. Similarly, it has been proposed that activation in older adults is less differentiated or focussed (e.g. Baltes and Lindenberger, 1997). Within our data, in contrast, there were activations which were bilateral for younger rather than older adults (e.g. Fig. 4, Lateral Occipital Cortex). Similarly, in areas where activation was shared by older and younger adults, activation was more diffuse for younger adults (e.g. precuneus, Table 2).

Before concluding, it is important to consider an alternative interpretation of the results. We found higher activation for preview search compared to Full Set Search in older compared to younger adults. This is equivalent to finding higher activity for Full Set Search than preview search in younger compared to older adults – i.e. effectively the opposite interpretation. Our results could therefore be interpreted to mean that frontal regions were more active in older adults for Full Set Search. This might suggest that neural compensation is particularly needed by older adults when the segmentation cues are absent. Whilst this is an interesting proposal, it does not explain how older adults are able to maintain performance in preview search despite declines in multiple related capabilities. We note that when analysed without the young adults, no frontal regions were identified as being activated for preview search for older adults (Fig. 4, Table 2). Older adults, on the other hand, appeared to have activation in more working memory and attention related regions.

The differences between older and younger adults appear in their connectivity and in contrasting patterns of activity in task specific areas (see Fig. 6). These differing patterns of activity are likely to stem from variations both in task and in participant's capacity. Schneider-Garces et al. (2010) found that both older and younger adults recruited additional and similar frontal and parietal brain regions when performing a memory task. Younger adults only recruited these regions when the task became difficult. Older adults recruited similar regions at a lower level of difficulty but their behavioural performance was noticeably worse than younger adults at these higher levels of difficulty. Furthermore, when corrected for working memory capacity, activation patterns were similar across the ages. Schneider-Garces et al. (2010) suggested that all adults recruit compensation mechanisms when task difficulty increases but this is then limited either by resources or capacity. Whilst the memory tasks used by Schneider-Garces et al. are quite different to our search tasks it should be noted that some of their compensation related regions (premotor and parietal regions) show greater activation in our older adults than our younger adults. It seems likely, therefore, that here older adults are using more working memory related resources to match younger adults' performance. Regions more activated in older adults are also regions which show decreases in activity with practice on working memory tasks (Garavan et al., 2000). This suggests that younger adults may rapidly become expert at the preview task, reducing activity and connectivity in some areas but maintaining it in others. Older adults may not (ever) be able to do so. The wide spread increases in activation in our study for older adults in posterior and occipital regions is consistent with a diffuse increase in attention or effort. It is an open question as to

whether older adults would eventually match younger adults' brain activation patterns and reduce this activation. Since we allowed all participants considerable practice we could not test if young adults' brain activation patterns initially match our older adults' patterns.

Conclusions

Despite well documented age-related perceptual decline, older adults are able to maintain the ability to select for ignoring a subset of the visual display defined by time. They are able to ignore earlier appearing distracters and use that to improve search performance. Brain imaging reveals, however, that the underlying brain mechanisms are quite different to those used by younger adults. In the initial, to be ignored, display, frontal regions appear to be more involved for older adults. This suggests a compensatory mechanism, perhaps to compensate for age-related declines in inhibition or suppression which continues to be connected throughout the task. Using our two display preview paradigm we show how this compensation can be enacted. When considering the entire preview search duration, older adults have more activation in visual and parietal posterior brain regions and distinct patterns of activity within these regions. Despite the compensatory activity at the start of the trial, older adults require more working memory and increased attention to benefit from preview.

Appendix A. Supplementary data

Supplementary data to this article can be found online at [doi:10.1016/j.neuroimage.2011.10.070](https://doi.org/10.1016/j.neuroimage.2011.10.070).

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