

Neural fate of ignored stimuli: dissociable effects of perceptual and working memory load

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Observers commonly experience functional blindness to unattended visual events, and this problem has fuelled an intense debate concerning the fate of unattended visual information in neural processing. Here we used functional magnetic resonance imaging (fMRI) to demonstrate that the type of task that a human subject engages in determines the way in which ignored visual background stimuli are processed in parahippocampal cortex. Increasing the perceptual difficulty of a foveal target task attenuated processing of task-irrelevant background scenes, whereas increasing the number of objects held in working memory did not have this effect. These dissociable effects of perceptual and working memory load clarify how task-irrelevant, unattended stimuli are processed in category-selective areas in human ventral visual cortex.

People show dramatic lapses in their ability to consciously perceive and remember unattended information¹. What is the fate of such unattended, unreportable visual information in neural processing? “Early selection” theories posit that attention acts as a filter that minimizes perceptual encoding of unattended events. Alternatively, a selection process might block conscious awareness of unattended stimuli at a later stage of processing, that is, after perceptual encoding (this is the “late selection” view). Several decades of research have yielded support for both early and late selection views of visual attention, indicating that both accounts have a certain degree of validity^{2–9}. The lack of consensus in the field, however, stems from the reliance on incomparably different tasks and stimulus configurations. One recently successful effort toward a unified account is perceptual load theory, which predicts that as more perceptual-spatial attention is allocated to a target, less attention becomes available to process background distractors^{10–12}. Accordingly, unattended background processing should occur under conditions of low perceptual load, but not under conditions of high perceptual load⁷.

Task difficulty can vary in several ways. Beyond perception, working memory is important for maintaining and manipulating representations of items that are out of view¹³. Such working memory functions are supported by enhanced neural activity for attended visual targets in a broad network of brain regions^{14–18}. However, a concurrent-object working memory task does not disrupt visual search: maintaining a load of multiple objects in visual working memory does not seem to impair the behavioral efficiency of locating a target among distractors¹⁹. Thus, the type of attention used to maintain and manipulate objects in working memory, which we refer to as central attention, may be separate from the type of attention used for visual-spatial selection, that is, perceptual attention^{12,20}.

The present study integrates these various insights toward a unified account of how task-irrelevant stimuli are processed. We used event-

related fMRI to investigate how increased perceptual demands and working memory load each influence perceptual processing of task-irrelevant stimuli in ventral cortex. We predicted and confirmed that increasing the perceptual demands, but not the working memory load, of a primary task weakens the neural representations of task-irrelevant background stimuli.

RESULTS

In the main experiment, subjects viewed composite face-scene stimuli (Fig. 1). The task was always focused on the face stimuli, which were presented at fixation and clearly segregated from the background scene with an outline border. Thus, subjects could use spatial attention to focus on the foveally presented face stimuli. Subjects were instructed to ignore the background scenes, which were always irrelevant to the face task.

Each fMRI run of the experiment had three face task conditions tested in separate blocks of trials. In the low-demand baseline condition, subjects performed a one-back repetition detection task of clearly visible faces presented in a rapid sequence within each trial. The faces appeared in the center of the composite face-scene stimuli presented for 500 ms each, and intervening masks were presented for 500 ms. Subjects were instructed to detect consecutive repetitions of identical face stimuli, while ignoring the background scenes. Face repetitions occurred in only 25% of trials, and to avoid confounding activity from face repetition detection, we focused our primary analyses on the remaining 75% of trials that did not contain face repetitions.

Independent of the face repetition manipulation, we also varied whether the background scenes were repeated or all novel during any given trial. Neural activity in response to repeated stimuli is weaker than that to novel stimuli, so an attenuation in the blood oxygen level-dependent (BOLD) signal to repeated versus novel background scenes provides an index of stimulus-specific processing²¹. Thus,

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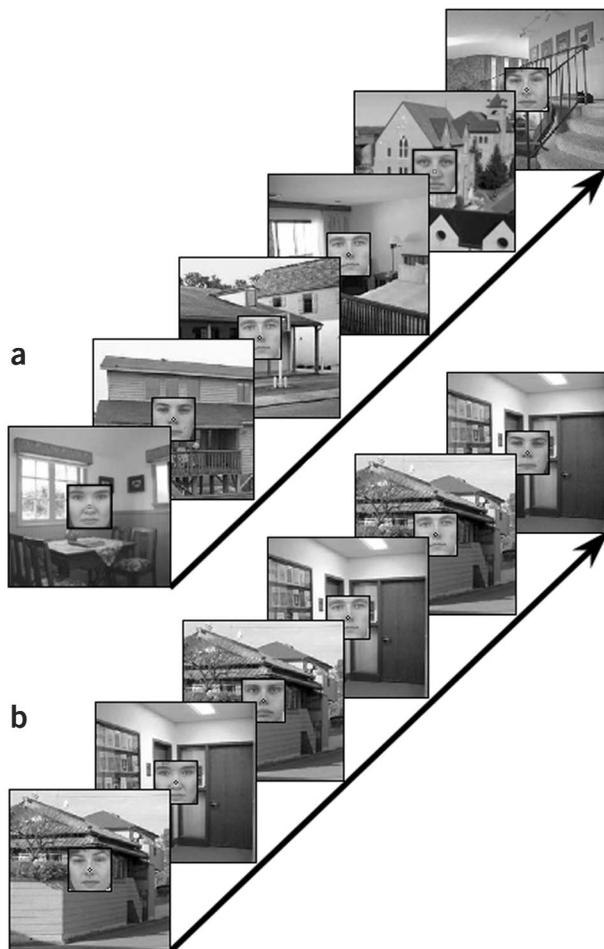


Figure 1 Primary task stimuli. The primary task presented a sequence of six composite images of a small face ($2.8^\circ \times 2.8^\circ$) occluding the center of a large scene ($9.8^\circ \times 9.8^\circ$), with a black frame segregating the face and scene. The composite images were interleaved with checkerboard masks (not shown here; see **Supplementary Videos 1 and 2** online or http://pantheon.yale.edu/~chun/demos/Yi_2004NN.html). **(a)** Example of the unrepeated-scene condition. **(b)** Example of the repeated-scene condition.

None of our subjects reported having noticed such alternation of scenes within a trial during the experiment. On unrepeated-scene trials, all of the six background scenes were novel. Within each block, repeated and novel scene trials were presented in a random event-related design.

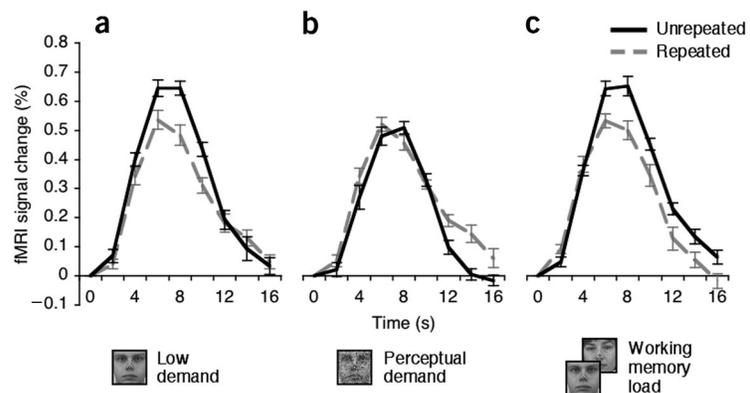
To assess how the background scenes were processed within the visual pathway, we focused our *a priori* fMRI analyses on the parahippocampal place area (PPA), a region of medial temporal cortex important for visual scene analysis²². The PPA responds strongly to scenes and negligibly to faces, allowing us to probe activity to background scenes that was not confounded by the face task. The PPA region of interest (ROI) was functionally localized within individual subjects in two independent scans conducted after the main experiment.

As shown in **Figure 2**, the results of the low perceptual demand baseline condition show that the BOLD signal in the PPA was significantly reduced to repeated scenes (**Fig. 2a**). This indicates that the task-irrelevant scenes were indeed processed in a stimulus-specific manner. In accord with perceptual load theory^{10,20}, spatial attention was not fully consumed by the face task. Thus, processing resources (perceptual attention) 'spilled over' to the background, allowing stimulus-specific attenuation as the background scenes were repeated within a trial.

If this interpretation is correct, then increasing the perceptual demands of the face task should reduce the amount of perceptual attention available for incidental background scene processing. We tested this hypothesis in the high perceptual demand condition by degrading the face stimuli with random salt and pepper noise to increase the difficulty of face discrimination. Indeed, face target detection performance dropped significantly (**Fig. 3**, compare white bars in **a** and **b**). Most importantly, the BOLD signal to unrepeated scenes in the PPA was significantly lower in the high perceptual demand condi-

comparing neural activations for repeated versus unrepeated scene stimuli reflects the extent to which perceptual and working memory load manipulations affect stimulus-specific processing of the background scenes. On repeated-scene trials, two different scenes were alternated so that each appeared three times throughout the trial.

Figure 2 fMRI signal change in the PPA ROI as a function of task type and background scene repetition. The insets schematize the type of tasks: one-back or two-back, clean or noisy. Black traces indicate PPA activity in unrepeated scene conditions, and dashed gray traces indicate PPA activity in repeated scene conditions. **(a)** Responses in the low-demand baseline conditions. **(b)** Responses in the high perceptual demand conditions. **(c)** Responses in the working memory load conditions. Unrepeated scene activation was lower in the high perceptual demand condition than in the other two conditions (all $t > 3.6$; all $P < 0.01$). Paired comparisons between the repeated and unrepeated scene conditions revealed significant differences in the low-demand baseline condition ($t = 2.946$, $P < 0.05$) and the high working memory load condition ($t = 4.152$, $P < 0.05$), but not in the high perceptual demand condition ($t = 0.170$, $P > 0.5$). Error bars indicate standard error (\pm s.e.m.).



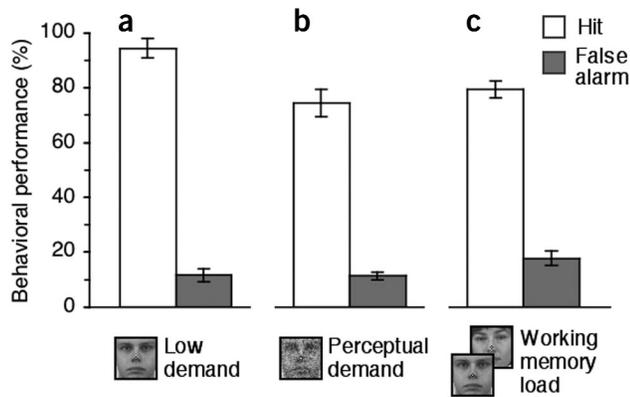


Figure 3 Behavioral results of the face repetition detection performance. (a) Results in the low-demand baseline condition. (b) Results in the high perceptual demand condition. (c) Results in the working memory load condition. Paired comparisons of the hit rates (white bars) revealed that subjects detected the repeated face target better in the low-demand baseline condition than in either of the higher-demand conditions (all $t > 2.4$; all $P < 0.05$). The hit rates of the two high-demand conditions were not different from each other ($t = 0.647$, $P > 0.5$). No significant difference was found in comparisons of the false-alarm rates (gray bars; all $t < 2.3$; all $P > 0.05$). Error bars indicate standard error (\pm s.e.m.).

tion than it was in the low perceptual demand condition (Fig. 2, compare black traces in a and b). Furthermore, the attenuation effect in the PPA to repeated versus novel scenes was abolished (Fig. 2b, no difference between solid black and dashed gray traces). Thus, the background scenes were not processed to the same extent as they were in the low perceptual load condition. In other words, increased perceptual demands of the primary face task filtered (attenuated) processing of the background scenes. Such filtering (withdrawal of perceptual visual-spatial attention) is mediated by the narrowing of neuronal receptive fields in temporal cortex^{23–25}, attenuating the neural response to novel images. This finding not only shows how the widely studied repetition suppression effect^{21,26,27} can be modulated by task demands^{28–31}, but it also suggests that the repetition suppression effect may be viewed as a novelty enhancement effect in the present task.

Does the attenuation in neural activity reflect spatial filtering or is it simply the result of increased task difficulty, as would be predicted by a monolithic view of attention? Several theories have advanced the view that attentional selection occurs at multiple stages throughout the brain as perceptual information is transformed to guide decisions

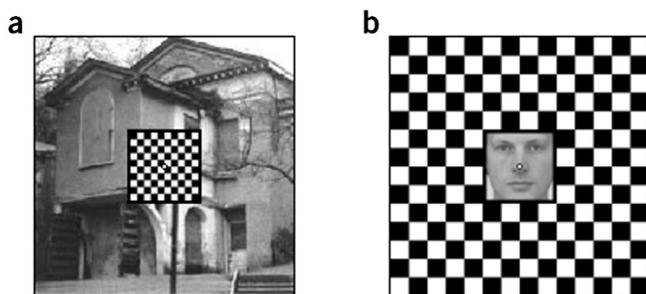


Figure 4 Examples of composite images used to localize the PPA ROI. (a) Scene image. (b) Face image.

and behavior^{12,20,32–34}. If the multiple-resource view is correct, then post-perceptual, central operations performed in working memory should not impact background scene processing in the same way that the perceptual load manipulation did.

Accordingly, our third task condition manipulated working memory load. Subjects performed the same face-repetition detection task used in the low-demand baseline condition, except that face repetitions occurred across two frames. This two-back repetition detection task required subjects to encode, maintain and compare more faces in working memory, and so naturally it was more difficult than the one-back task. A whole-brain analysis revealed significantly higher activation for the two-back task compared to the one-back task in prefrontal cortex (see Methods), which is consistent with prior working memory studies³⁵.

To facilitate comparison between the perceptual difficulty and working memory load manipulations, performance in the high perceptual demand condition was matched with each individual subject's performance in the two-back task (see Methods). Face repetition detection performance was similar in the high working memory load and the high perceptual demand conditions (Fig. 3). Unlike the high perceptual demand manipulation, however, increasing working memory load did not influence background scene processing (Fig. 2c), as the overall level of activity was comparable with the low-demand baseline condition (Fig. 2a). In addition, there was a significant attenuation effect in the PPA to the repeated versus novel background scenes, suggesting that the background scenes were fully processed during high working memory load. In other words, even though the two-back task greatly increased the difficulty of the face task, this had no effect on perceptual processing of task-irrelevant background scenes as when working memory load was low. Thus, perceptual demand manipulations and working memory load manipulations had strikingly different effects on the processing of the visual background.

DISCUSSION

In conclusion, our study demonstrates that neural processing of unattended stimuli depends on the task that the observer is primarily engaged in, suggesting a unified resolution to the classic early versus late selection debate. Perceptual, visual-spatial attention focuses processing on a target stimulus to the exclusion of task-irrelevant events, resulting in early selection⁷. Although such perceptual-spatial attention mechanisms may be tied to spatial working memory processes^{36–38}, our work distinguishes such perceptual mechanisms of selection from central attention (control) mechanisms involved in the consolidation, maintenance and manipulation of object representations in visual working memory²⁰. We suggest that perceptual encoding of unattended distractors (late selection) may routinely occur across different loads of object working memory. This proposal ties together various studies that demonstrate late selection in a broad array of tasks that manipulate central attention, such as distractor exclusion³, attentional blink^{4,5} and the psychological refractory period^{6,39}. In fact, distractors that further impose response conflict may reveal not only late selection, but increased distractibility under conditions of high working memory load or prefrontal lobe damage. This prediction has been confirmed in neuropsychological⁴⁰, behavioural^{20,41} and neuroimaging work³. These findings are compatible with the present results in that all these studies exhibit late selection under variations of working memory load and prefrontal control.

Altogether, our results speak against the common misconception of attention as a unitary resource. Instead, attention should be under-

stood as a competitive process embedded within more specific perceptual selection and cognitive control subsystems^{12,20,32–34}. The act of attending recruits different processes depending on the task, and the present study demonstrates how the type of attention engaged determines the extent to which unattended visual events leave stimulus-specific neural traces in high-level perceptual cortex.

METHODS

fMRI data acquisition. Nine paid subjects (6 females, 21–31 years old) were scanned in a 3T whole-body GE/Magnex scanner. Informed consent was obtained, and the study protocol was approved by the Vanderbilt University Institutional Review Board. Anatomical images were acquired using conventional parameters. T2* scan parameters were as follows: repetition time (TR), 2 s; echo time (TE), 25 ms; flip angle (FA), 70°; 229 images per slice, with 19 axial slices (7 mm thick, 0 mm skip) acquired parallel to the anterior commissure–posterior commissure (AC–PC) line. Stimuli were presented through LCD goggles (VisuaStim XGA, Resonance Technology). Images for each subject were realigned to correct for head motion using SPM99 (Wellcome Department of Cognitive Neurology, Institute of Neurology, London, UK).

Task design and procedure. All subjects completed five runs of the attend-face, ignore-scene task, each of which consisted of three different types of eight-trial blocks: low-demand baseline blocks, high perceptual demand blocks, and high working memory load blocks. In each eight-trial block, six trials had no face repetition (target-absent). In three of these target-absent trials, the background scenes were all novel, whereas in the other three trials, two background scenes alternated across frames within each trial. There were also two face-repetition (target-present) trials in each block and during one of these trials the background scene also repeated. The same set of faces was used in all runs, whereas scenes always differed across trials and runs.

Each event-related trial was preceded by a 400-ms fixation point, which remained on the screen throughout the trial. Twelve images were then presented in a serial manner. Six scene-face composites were interleaved with checkerboard masks. The element size of each checkerboard was roughly scaled to eccentricity, such that faces were masked by small elements (0.28° × 0.28°) and scenes by large elements (0.7° × 0.7°) (see **Supplementary Videos 1 and 2** online or http://pantheon.yale.edu/~chun/demos/Yi_2004NN.html). Each image was presented for 500 ms without blank interstimulus intervals. Subjects reported whether or not a face repeated by pressing a button on a handheld key box within 3 s after the disappearance of the last frame. After the response collection, there was an 8.2-s fixation period during which the fixation point changed to either 'one' (for the one-back task in the low and high perceptual demand blocks) or 'two' (for the two-back task in the high working memory load block). This served to remind subjects of the task they were performing. The next trial began 400 ms after the fixation signal was turned off (total trial duration = 18 s). Before each run, the noise level of the random salt and pepper noise mask used in the high perceptual demand blocks was adjusted based on the performance of the two high-demand blocks in the previous run in order to titrate the difficulty of those two conditions (average noise level across all subjects was 19% as shown in **Fig. 2b**).

In the last two PPA localizer runs, subjects performed repetition detection of faces or scenes in alternating blocks^{5,22}. To maximize comparability, the sizes of faces and of scenes were the same as those in the main task (**Fig. 4**).

fMRI data analysis. Analyses were conducted with the Yale fMRI software package (<http://mri.med.yale.edu/individual/pawel/fMRIpackage.html>) and custom Matlab scripts (Mathworks).

The PPA was localized in each individual by contrasting the averaged brain activity in scene blocks with face blocks of the localizer task. Statistical parametric maps of BOLD activation for each subject were created using a skew-corrected signal difference (measured as a percent change). The PPA ROI was defined as the voxel with the peak activation and its eight surrounding voxels from each hemisphere^{5,42}. All subjects showed an active region in the parahippocampal gyrus/collateral sulcus region, consistent with prior studies^{22,42} (mean Talairach coordinates: $x = 24$, $y = -57$, $z = -5$; $x = -25$, $y = -61$, $z = -5$).

For each ROI of each subject, the BOLD signal change in the attend-face, ignore-scene task was calculated by averaging the time courses of each of six conditions (3 task types × 2 scene repetitions) and normalizing them to the activation of the first volume acquired after trial onset. ROI time courses were collapsed between both hemispheres and then averaged across all subjects. Statistical analyses (repeated-measures ANOVA and paired *t* tests) between conditions were performed on the average of the fourth and fifth volumes after trial onset as the peak amplitude response, which was first determined by collapsing all six conditions together (see also **Fig. 2**). There were significant main effects of task type ($F_{2,16} = 4.720$, $P < 0.05$) and of scene repetition ($F_{1,8} = 9.514$, $P < 0.05$), as well as an interaction between these factors ($F_{2,16} = 6.144$, $P < 0.05$). Area under the curve analyses confirmed these results. In addition, we confirmed in an additional subject that these observed modulations in the PPA reflect modulation of scene processing rather than the manipulations of the face task *per se*. In other words, degraded versus clean faces had negligible influence on PPA activity when presented alone without background scenes.

Whole-brain analyses examined significant activity beyond the PPA ROI using an uncorrected threshold of $P < 0.0001$. Compared with the low-demand baseline, there were no significant differences in the high perceptual demand condition, whereas higher activity was observed for the high working memory load condition in the right medial frontal sulcus ($x = 44$, $y = 17$, $z = 23$), left inferior frontal sulcus ($x = -39$, $y = 22$, $z = 16$) and bilateral precuneus ($x = -3$, $y = -55$, $z = 50$; $x = 7$, $y = -48$, $z = 41$).

Note: Supplementary information is available on the Nature Neuroscience website.

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COMPETING INTERESTS STATEMENT

The authors declare that they have no competing financial interests.

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