

# Top–down biases win against focal attention in the fusiform face area

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Many studies have reported that BOLD activity in visual cortex is enhanced in the presence of selective attention. These reports are seemingly at odds with psychophysical data showing that observers are able to efficiently categorize natural stimuli in the near-absence of focal attention. To reconcile these two lines of evidence, we study the effects of attentional modulation on face-selective responses in the fusiform face area (FFA) using fMRI. Different from previous fMRI studies in which an “attended” condition (where subjects make a behavioral report on faces) is compared to an “unattended” condition (where the faces are task irrelevant), we included a third condition in which focal attention was not fully available to the faces yet they remained task relevant. Thus we were able to distinguish between the effects of spatial attention and a task-based component of attention. Whether or not subjects had to spatially attend to the faces made no difference to the amplitude of BOLD activity in the FFA provided the faces had to be discriminated. As expected, we observed a decrease in BOLD activity in the FFA when faces were task irrelevant. This pattern of modulation of the BOLD response as a function of the subject’s behavior was region specific as it did not extend to the parahippocampal place area. These results point to a coherent picture of how spatial attention and top–down task-based attention interact in visual cortex.

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## Introduction

How does the visual system handle unattended objects? Evidence from “change blindness” studies demonstrates that fairly large changes to scenes can often escape awareness when attention is not directly focused on them (Rock et al., 1992; Simons and Levin, 1997). These results are supported by fMRI studies showing that BOLD activity for unattended or unseen objects is decreased or even abolished in high-level areas specifically encoding these stimuli (Wojciulik et al., 1998; O’Craven et al., 1999; Bar et al., 2001; Vuilleumier et al., 2001a,b; Pessoa et al., 2002; Marois et al., 2004; Yi et al., 2004). On the other hand, recent psychophysical

evidence suggests that natural objects and scenes can be categorized in the near-absence of focal, spatial attention (Li et al., 2002; Rousselet et al., 2002; Reddy et al., 2004; Rousselet et al., 2004a,b; Fei-Fei et al., 2005). For example, using a dual-task paradigm (Sperling and Melchner, 1978; Braun and Sagi, 1990; Braun and Julesz, 1998), we showed that subjects performed a face–gender discrimination task efficiently when focal attention was not fully available (Reddy et al., 2004). Performance on this task was only minimally impaired when attention was withdrawn by another attentionally taxing task. In the present study we used the same dual-task paradigm inside a 3.0 T magnetic scanner in an attempt to reconcile these seemingly contradictory observations.

Previously, fMRI studies have investigated the effects of attentional modulation on face processing as paradigmatic for object processing in general (Wojciulik et al., 1998; O’Craven et al., 1999; Vuilleumier et al., 2001a,b; Pessoa et al., 2002). Many of these studies compared activity in the fusiform face area (FFA) (Kanwisher et al., 1997; Kanwisher et al., 1999) in two conditions: when the faces were fully attended and task relevant, or when the faces were fully ignored (and task irrelevant). Differences in BOLD activity between these two conditions were attributed to attentional modulation. However, because subjects were instructed to make a behavioral report on the faces in the first, but not in the second condition, it is unclear whether the observed drop in activity is solely due to the modulation of spatial attention or if it can also be explained by a change in a non-spatial top–down attentional component, which arises as a result of different task-based instructions in the two conditions (we consider this task-based attentional component to be non-spatial based on the assumption of a unique spatial focus of attention (Posner et al., 1980)). This non-spatial form of attention, which we will operationally term ‘top–down task-based attention’, could be related to feature-based and/or object-based attention—provided one assumes that a face constitutes a feature or object for the visual system (O’Craven et al., 1999; Treue and Martinez Trujillo, 1999).

The purpose of our study was to tease apart the relative contribution of these two attentional components (focal spatial attention and top–down task-based attention) to the modulation of FFA BOLD signals. Some studies have already examined the effect of manipulating focal attention for task irrelevant face stimuli (O’Craven et al., 1999; de Fockert et al., 2001; Downing et al.,

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2001), and as mentioned earlier other studies have manipulated both factors together. But the specific effect of task relevance and the way it might interact with spatial attention is unknown. Here we ask how task-based attention influences BOLD activity in the near-absence of spatial attention. To address this issue, it is necessary to employ an attentional paradigm in which both forms of attention are manipulated separately. An advantage of the dual-task paradigm is that, in addition to the two conditions used in most previous studies (faces attended vs. faces ignored), it includes a third condition in which attention is spatially focused away from the faces (on an attentionally demanding letter discrimination task), yet they remain task relevant. Thus we are in a position to separately examine the effects of focal attention and task-based attention on activity in the FFA. In agreement with previous reports, we observed a significant drop in activity when the faces were unattended (both in terms of focal spatial attention and task-based top-down attention). However, when spatial attention was directed away from the faces, but they remained task-relevant, activity was left unaffected. Thus, top-down biases can overcome limitations due to a lack of spatial attention.

## Methods

### *Behavioral training*

Twelve paid volunteers, aged 20–30, participated in the experiments. All experiments were conducted according to the guidelines of the Institute's committee for protection of human subjects. We used a dual-task paradigm to examine the effects of attentional manipulation. Subjects performed two tasks—either alone (single-task conditions) or concurrently in the dual-task condition, yielding a total of three conditions. One of these tasks consisted of face–gender discrimination while the other was a five letter (T/L) discrimination task known to engage spatial attention (Braun and Julesz, 1998; Lee et al., 1999; Li et al., 2002). Each trial began with a fixation cross presented for  $300 \pm 100$  ms before the onset of the first stimulus. At 0 ms, 5 randomly rotated letters (Ts or Ls) were presented at 9 possible locations within  $1.2^\circ$  of fixation. A face subtending approximately  $2.5^\circ$  of visual angle then appeared at a random location on an imaginary rectangle subtending  $8^\circ \times 10^\circ$  of visual angle. The eccentricity of the center of the faces was thus between a minimum of  $4^\circ$  and a maximum of  $6.4^\circ$ , measured along the diagonal. The faces were backward-masked by a pattern mask composed of scrambled faces, following which the letters were backward-masked with an “F” rotated by an angle corresponding to the letter it replaced (Fig. 1a). Depending on instructions given at the beginning of the block, subjects either performed the peripheral (face–gender) or central (letter discrimination—subjects had to report if the letters were all the same or not) tasks alone or both tasks together (dual-task). Subjects were always instructed to maintain their gaze on the central letter task. In the dual-task condition they were told to prioritize the letter task and make the behavioral report first on the letter task at the end of each trial. The face stimuli (obtained from the MPI, Tübingen, Germany) contained seven views of 100 male and 100 female faces and were well matched for low-level features such as color, size and illumination. Since pilot experiments had shown that the gender of some faces in the database was ambiguous (overall discrimination performance of 65%), we used the 50 male and 50 female individuals who produced the highest discrimination performance. For details, see Reddy et al., 2004.

To examine the effects of training on brain activity two groups of subjects, trained and untrained, were used. The six “trained” subjects were trained on the two single-task conditions as well as the dual-task condition while the six “untrained” subjects were trained on only the two single-task conditions. The entire training procedure typically lasted between 5 and 10 h on consecutive days for each subject and was carried out outside the scanner on a Silicon Graphics computer. At the beginning of training, the letters were displayed for 500 ms and the faces for 160 ms before the masks appeared. During training, for each subject, the SOAs were decreased independently for both tasks when performance on a 48-trial block exceeded 90%. Training was complete when subjects’ “letter” SOA had stabilized below 250 ms. Over the group of 12 subjects, the SOAs varied between 146–183 ms and 183–240 ms on the face and letter tasks respectively. An auditory tone was provided as feedback on incorrect trials.

To control for whether the central letter discrimination task was sufficiently demanding to engage the focus of attention away from the periphery, we performed a separate control experiment with the “trained” subjects. In this control the peripheral task involved discriminating a vertically bisected disk with red and green halves (equated for gray values) from its mirror image. Each disk was masked by a disk divided into four red and green alternating quadrants. Subjects received equal amounts of training on this task (central, peripheral and dual blocks) as on the face–gender discrimination task; the tasks were matched for difficulty such that average single-task performance was around 80%. The disks were of the same size and presented at the same eccentricity as the face stimuli in the main experiment.

Normalized behavioral performance values are reported in Fig. 2 and were calculated by a simple linear scaling of the mean value of each participant's performance. The scaling mapped the mean single-task performance to 100%, leaving chance at 50%:  $\text{normalized performance} = 0.5 + 0.5 \cdot [(P_2 - 0.5) / (P_1 - 0.5)]$ , where  $P_2$  and  $P_1$  refer to performance in the dual-task and single-task conditions respectively.

### *fMRI sessions*

Both trained and untrained subjects performed the face–gender dual-task experiment in a 3.0 T whole-body Siemens scanner at the California Institute of Technology. Stimuli were produced on a Macintosh laptop and viewed through optical goggles (Resonance Technologies, Northridge, CA, VisuaStim XGA,  $800 \times 600$  resolution at 60 Hz). The size and eccentricity of the stimuli in the goggles were the same as that during training. T2\* weighted echo-planar images (TR=2 s, TE=30 ms, FA=90°, FOV=210 mm,  $31 \times 3$  mm interleaved axial slices) were acquired using the whole-head coil and an in-line motion correction sequence (Thesen et al., 2000). The slices were positioned to cover the temporal lobe. Each functional run consisted of 186 volumes; the first two volumes were discarded. A 12-minute high resolution ( $1 \times 1 \times 1$  mm) whole-head T1-weighted MPRAGE sequence (T1=1.5 s, TI=0.8 s, TE=3.05 ms, 176 sagittal slices) was also acquired for each subject.

### *Localizer task*

Subjects were first presented with sequences of images in order to localize the FFA (Kanwisher et al., 1997). The design consisted of alternating 30 s blocks of faces and scenes (approximately  $9 \times 13.5^\circ$  of visual angle, obtained from the Vision

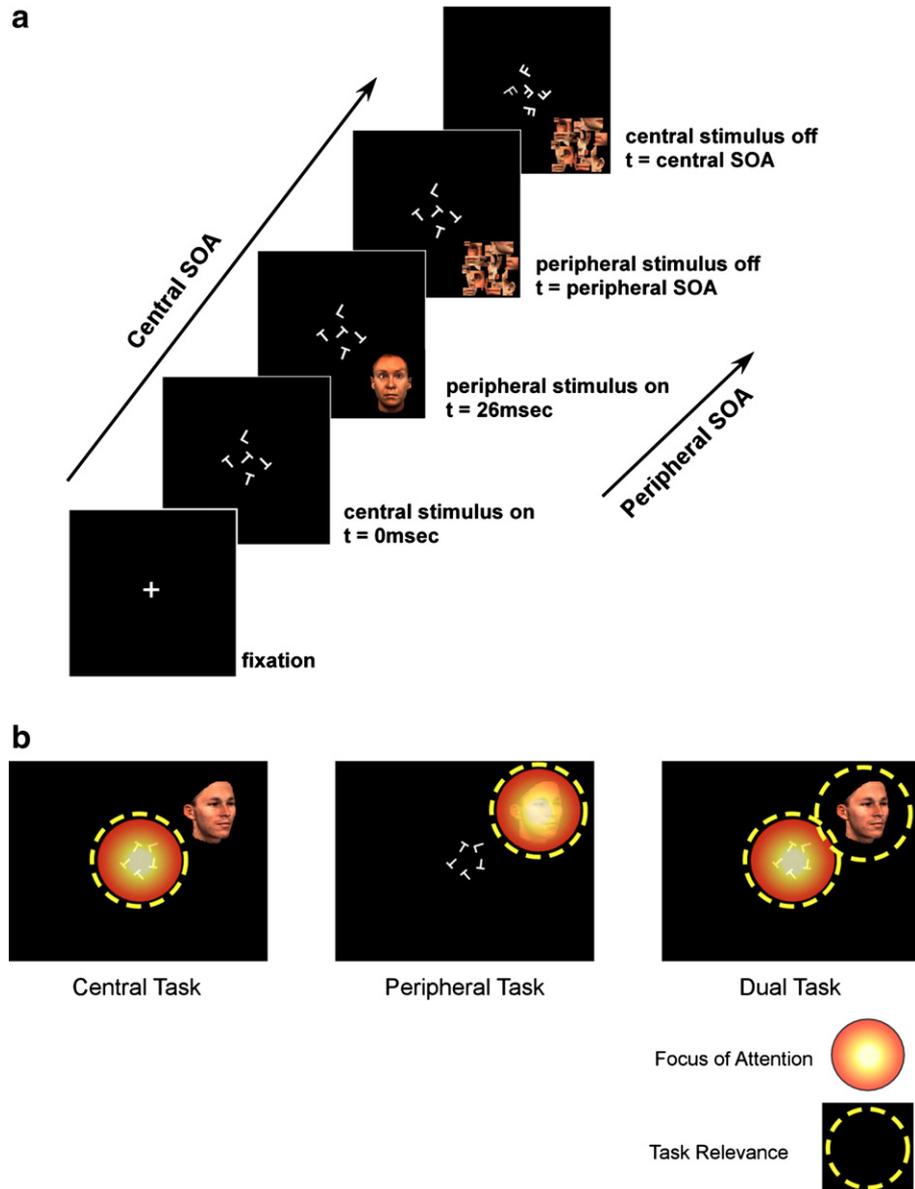


Fig. 1. (a) Schematic timeline for a typical trial in the dual-task experiment. At the end of the trial, subjects are required to report the gender of the face presented and/or whether the letters were all the same or different. The layout was the same for all trials, independent of specific instructions given to subjects at the beginning of each block. Central SOA ( $\sim 200$  ms) and peripheral SOA ( $\sim 160$  ms) indicate the presentation time for letters and faces respectively. The faces appeared at random locations on an imaginary rectangle subtending  $8^\circ \times 10^\circ$  of visual angle. (b) A schematic, simplified explanation of the manipulation of the focus of attention and top-down task-based attention in the 3 conditions of the paradigm. In the central-task condition, the spatial focus of attention is on the letters. Since subjects report only on the letters, the faces are behaviorally irrelevant. In the peripheral-task condition, spatial attention is available to the faces, and the faces are also task-relevant. In the dual-task condition, the spatial focus of attention is shifted away from the faces, yet they remain task relevant since subjects are required to make a report on them. Thus, these three conditions enable us to tease apart the effects of these two factors. Note that the visual input is exactly the same in all three conditions. What changes is the task subjects have to perform.

Lab at Caltech (<http://www.vision.caltech.edu/html-files/archive.html>) presented for 1 s each at fixation. The faces were different from the ones used in the dual-task experiment (see above). Each run lasted for 4 min and subjects participated in 3 runs. The FFA and PPA ROIs were localized in each individual by contrasting average brain activity in face versus scene blocks. Due to different signal-to-noise ratios, there was some variation in the threshold used for defining the ROIs across subjects. The average  $t$  value that defined the ROI was  $t(6) = 4.1 \pm 0.4$ . The mean Talairach

coordinates of the FFA and PPA (right FFA:  $x = 38 \pm 1$  mm,  $y = -50 \pm 2$  mm,  $z = -13 \pm 1$  mm; left FFA:  $x = -40 \pm 1$  mm,  $y = -51 \pm 2$  mm,  $z = -15 \pm 2$  mm; right PPA:  $x = 24 \pm 2$  mm,  $y = -42 \pm 2$  mm,  $z = -6 \pm 1$  mm; left PPA:  $x = -28 \pm 1$  mm,  $y = -46 \pm 4$  mm,  $z = -9 \pm 2$  mm) are consistent with previous reports (Kanwisher et al., 1997; Epstein et al., 2003). The FFA was also localized in a second experiment in which four of the six trained subjects were presented with a rapid stream of faces and scenes at peripheral locations. The faces used in this experiment were the same as

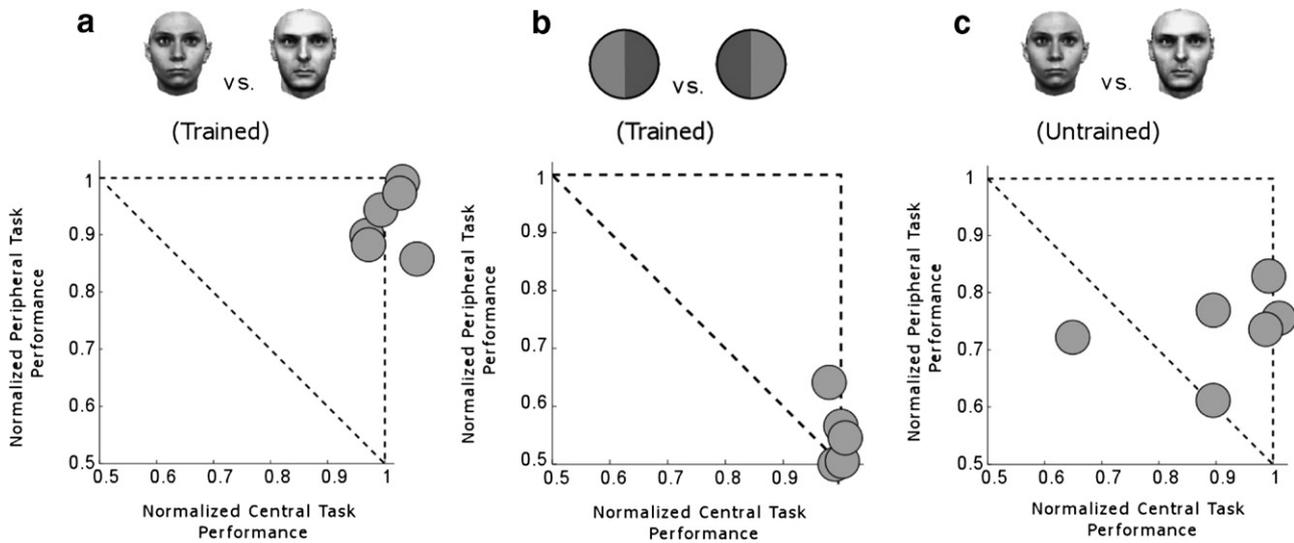


Fig. 2. Dual-task performance relative to performance achieved in the single-task conditions. (a) Face–gender discrimination performance for six trained subjects obtained in the scanner. Each point represents a subject’s dual-task performance on the central and peripheral tasks relative to their single-task performance on these tasks. This group of subjects achieves a high level of performance (average performance in the dual-task condition:  $92.5 \pm 2.0\%$ ). (b) Performance for five of the same subjects on a known attentionally demanding disk discrimination task (outside the scanner) falls to chance levels ( $55.3 \pm 2.5\%$ ) in the dual-task condition. Thus, the central task is effective in withdrawing focal attention away from the periphery. (c) Face–gender performance for six new untrained subjects obtained in the scanner ( $73.7 \pm 3.0\%$ ). As expected, we observe a significant drop in performance for these subjects in the dual-task condition.

those used in the dual-task experiment described above. Faces and scenes were presented at 5 Hz at peripheral locations identical to those at which faces were shown during the dual-task experiment. Subjects were asked to fixate on a central fixation cross. At any given peripheral location, 12 faces were shown for 200 ms each before a new location was chosen. The faces and scenes were presented in blocks of 40 s with 20 s blank intervals between blocks. With the exception of the rapid presentation of the face stimuli, the timing of this experiment thus mimicked that of the dual-task experiment described below. The FFA was localized in each individual by contrasting brain activity in face versus scene blocks and overlapped with the FFA identified during the main localizer experiment.

#### Retinotopic mapping

We used a slowly expanding checkerboard ring-flickering at 8 Hz to map eccentricity in the retinotopic occipital areas in three subjects following a well-established method (Engel et al., 1997). Each scan comprised 8 expansion cycles, with a cycle period of 40 s. Average activity corresponding to the stimulation between 0 and  $1^\circ$ , and between  $3.6$  and  $6.7^\circ$  radii were used to localize the central and peripheral ROIs respectively in each individual.

#### Dual-task paradigm

Subjects performed 10 runs of the dual-task paradigm in the scanner using the parameters described above except for the following modifications. In a single run, 2 blocks each of the central-, peripheral- and dual-task conditions were presented in a randomized counterbalanced order, with each block consisting of 16 trials. On average each block lasted approximately 40 s and was followed by a 20 s blank interval. Subjects made their behavioral report using a 4-button response box.

#### Data analysis

For each subject, images were co-registered between runs using a Linear Image Registration Tool (FLIRT) (Jenkinson et al., 2002). Analyses were conducted using custom Matlab software (Mathworks). For each subject, the time-course in the 3 task conditions was calculated by averaging the BOLD signal change in all voxels of the relevant ROI over all repetitions of each condition (after removing linear drifts over the course of each run). These time-courses were collapsed across hemispheres and subjects. These are the data shown in Figs. 3a, c and 4a, c. The time-courses for each subject were then averaged over the duration of the 40 s block (shifted by 7 s to account for the delay in the hemodynamic response) and normalized by dividing by the mean activation over all 3 conditions (group data shown in Figs. 3b and 4b). Statistical analyses (ANOVA and paired *t*-tests corrected for multiple comparisons using Scheffe’s method) were performed on these values.

## Results

#### Behavioral performance

We used a dual-task paradigm to examine the effects of attentional manipulation on brain activity in the FFA. As described in the Methods section, subjects performed a face–gender discrimination and a five letter discrimination task known to engage spatial attention (Braun and Julesz, 1998; Lee et al., 1999; Li et al., 2002). A typical trial is shown in Fig. 1a.

In all trials, both the face and letters were displayed as shown, and depending on instructions, subjects could perform one of three tasks: (1) in the peripheral face–gender task condition, subjects had to report whether the face was male or female. Since attention was focused on the faces, and subjects made a behavioral report on

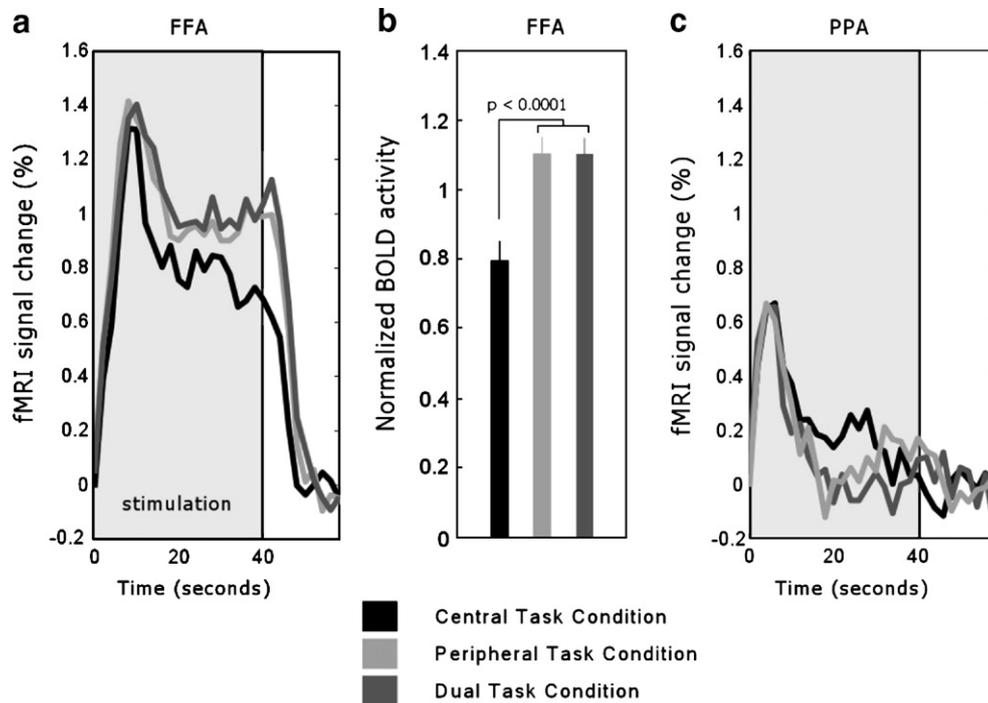


Fig. 3. BOLD activity for six trained subjects in the three conditions illustrated in Fig. 1b. (a) Time-course of FFA activity plotted as a function of time in the central-, peripheral- and dual-task conditions. (b) The same data shown in a summary format—the time-courses for each subject from panel a were averaged over the duration of the 40 s block (shifted by 7 s to account for the delay in the hemodynamic response) and normalized by dividing by the mean activation over all 3 conditions. The data show a significant drop in activity in the central-task condition compared to the peripheral-task condition. However, there is no significant drop in activity in the dual-task condition. Thus, simply removing the focus of attention from the faces does not affect activity. In contrast, making the faces task-irrelevant results in a significant decrease in the signal. (c) Activity in the PPA. The trend observed in the FFA is not observed in other high-level cortical areas, thus ruling out the possibility that the observed effects are due to general arousal.

them, this condition corresponds to the “attended” condition of most previous studies. (2) In the central letter task condition, subjects reported whether the letters were all the same or if one differed from the other four. In this condition, spatial attention is focused on the letters, away from the faces which are task irrelevant. Thus this task is similar to the “unattended” condition in previous studies. (3) In the critical dual-task condition, subjects had to perform on both tasks simultaneously. As we have shown previously (Reddy et al., 2004) and discuss below, in this condition, focal attention is not fully available to the faces although subjects are required to make a behavioral report on them. Thus, this condition allows us to distinguish between the effects of spatial attention and top-down task-based attention (Fig. 1b).

Six subjects who had been previously trained on the dual-task paradigm performed the central-, peripheral- and dual-task conditions in the scanner. The behavioral results for these subjects on this task are shown in Fig. 2a. As reported previously (Reddy et al., 2004), participants’ performance on face–gender discrimination in the dual-task condition was comparable to that obtained in the single-task condition (mean performance  $\pm$  s.e.m. normalized to single-task performance:  $92.5 \pm 2.0\%$ ). Thus, a high level of performance is achieved even in the near-absence of spatial attention. This conclusion also holds if we use  $d'$  as a response bias-free measure of performance:  $d'$  in the dual and single task conditions was on average  $1.8 \pm 0.5$  and  $1.4 \pm 0.3$  respectively and was not significantly different ( $p=0.15$ ). Similarly  $d'$  values were not significantly different between single- and dual-task conditions of the central task ( $p=0.1$ ). Eye movements do not play a major

role in achieving this performance since the peripheral faces are presented only briefly and at random locations (see Methods). Furthermore, control experiments with an eye-tracker have allowed us to verify the absence of eye movement contribution to this performance (Supplementary material).

An obvious concern that arises, however, is whether the central letter discrimination task is sufficiently demanding to engage the focus of attention away from the periphery. This concern can be addressed by verifying that performance on known attentionally demanding tasks suffers under the same dual-task conditions. As shown in Fig. 2b, performance for five of the subjects (the remaining subject was not available for testing) on a bisected disk discrimination task in the periphery falls dramatically when performed concurrently with the central letter task, even though their performance on this task was comparable to face–gender performance when both tasks were performed alone. The difference in  $d'$  values on this task between peripheral- ( $1.9 \pm 0.2$ ) and dual-task ( $0.25 \pm 0.1$ ) conditions was significant ( $p < 0.00005$ ) thus demonstrating that the central letter task did effectively engage the focus of attention away from the periphery. We thus define focal attention operationally as that resource which, when engaged by the central T/L discrimination task, is unavailable to the periphery, consequently impairing performance on some concurrent tasks (such as bisected disk discrimination, but not face–gender discrimination or natural scene categorization; see also Braun and Julesz, 1998; Lee et al., 1999; Li et al., 2002). Note that significant decreases in dual-task performance were also observed on an inverted face–gender discrimination task in which the same

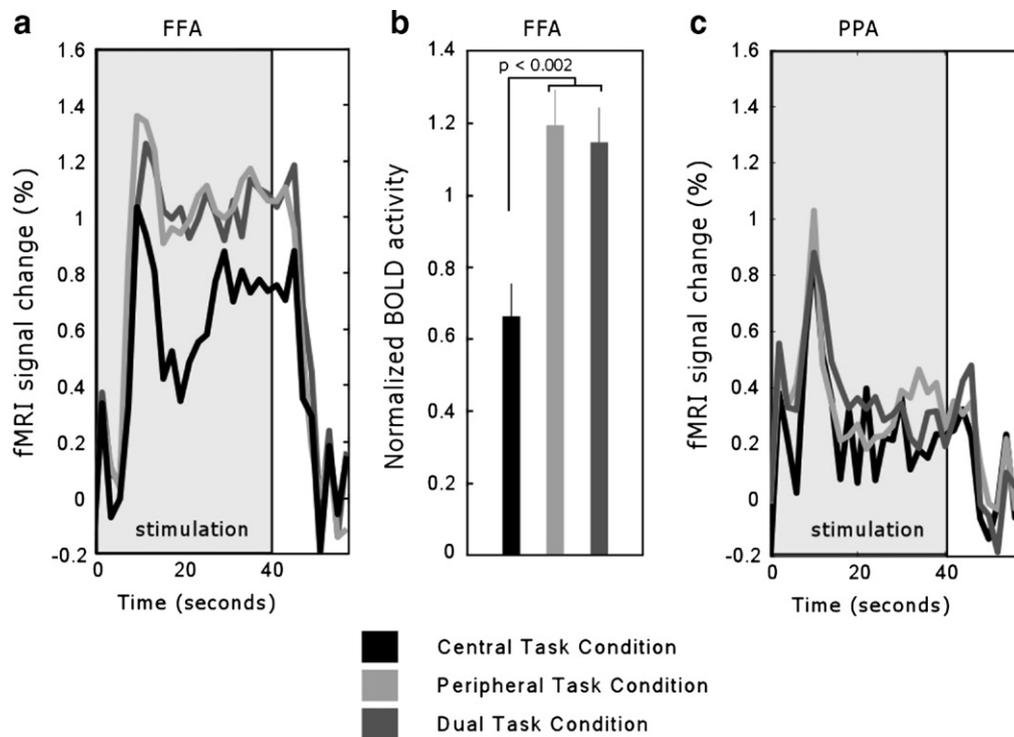


Fig. 4. BOLD activity for six untrained subjects in the experiment. (a) Time-course of FFA activity. Similar to Fig. 3, simply shifting the focus of attention from the peripheral faces to the central letters does not reduce the BOLD signal. What reduces the signal is making the faces task-irrelevant. (b) The same data shown in a summary format for the 3 conditions, similar to Fig. 3b. Note that despite the substantial drop in behavioral performance in the dual-task condition (Fig. 2c), no corresponding decrease in BOLD activity is observed in this condition. (c) Activity in the PPA. The trend observed in the FFA is not observed in other high-level cortical areas, thus ruling out the possibility that the observed effects are due to general arousal.

face stimuli were used as in the present study and were presented for similar SOAs (Reddy et al., 2004). Hence the central T/L discrimination task can, under some conditions, reduce performance even on face stimuli.

#### fMRI activity: main result

The FFA and the parahippocampal place area (PPA) (Epstein and Kanwisher, 1998) of each subject were isolated in separate localizer scans. The BOLD activity during the dual-task experiment was analyzed separately in the isolated FFAs from the left and right hemispheres. Since similar results were observed in both hemispheres, in the data presented here, the FFAs were collapsed across hemispheres. Fig. 3a shows the raw time-course of BOLD activity in the FFA during the three experimental conditions for the trained subjects. A one-way ANOVA revealed a significant effect of the attentional condition on BOLD responses [ $F(2,15)=11.89$ ,  $p=0.0008$ ]; post-hoc multiple comparison tests (Scheffe's method,  $p<0.05$ ) revealed that activity in the central-task conditions was significantly lower than in the peripheral- and dual-task conditions. Thus, consistent with previous reports, we observed a significant decrease in activity when the spatial focus of attention was removed from the faces and they were ignored (peripheral-task condition vs. central-task condition, Fig. 3b). Remarkably, in the dual-task condition, when attention was not focused on the face, but a gender-specific response was still required, activity was as high as in the peripheral-task condition. Thus, we observed a dissociation between the effects of focal attention manipulation per se and top-down task-based attention.

To rule out the possibility that BOLD activity was saturated in the peripheral- and dual-task conditions (thereby accounting for the similar levels of activity in these conditions), we compared FFA peripheral-task activity with that evoked by face stimuli during a second localizer experiment, in which four of the trained subjects were presented with a rapid stream of faces and outdoor scenes at 5 Hz at identical peripheral locations as during the dual-task experiment (see Methods). We observed significantly lower levels of activity in the peripheral-task condition compared to this second localizer experiment (mean  $\pm$  s.e.m.:  $1.0 \pm 0.1$  vs.  $2.1 \pm 0.4\%$  signal change respectively,  $p<0.05$ ). Thus the similar levels of activity observed between the dual and peripheral-task conditions truly mirror the experimental manipulation rather than a saturation in the BOLD signal.

In contrast to a recent study which reported total absence of activation to unattended and ignored faces (Pessoa et al., 2002), we observed decreased but significant levels of activation in the central-task condition, presumably in response to the peripheral and task-irrelevant faces (Figs. 3a, b). We estimated the amount of activation elicited by the faces in this condition by examining the effect of removing the faces altogether. In a control experiment, three of our trained subjects performed the letter discrimination task exactly as in the central-task condition with the exception that the faces were not presented in the periphery. We observed a large (67%) and significant ( $p<0.05$ ) drop in FFA BOLD activity when the faces were not presented compared to the central-task condition when the faces were present although unattended and fully ignored. Thus, we find that even unattended and ignored faces produce significant ( $p<0.05$ ) levels of FFA activation, in agreement with previous

reports (Wojciulik et al., 1998; Vuilleumier et al., 2001a,b). Furthermore, in comparing the BOLD signal in the FFA from the two localizer experiments in which faces and scenes were either presented centrally or at peripheral locations, we observed comparable levels of activation ( $1.9 \pm 0.2\%$  and  $2.1 \pm 0.4\%$  respectively;  $p > 0.05$ ). Although it has been suggested that the FFA is associated with a central visual field bias (Levy et al., 2001; Malach et al., 2002; Hasson et al., 2003), these results indicate that peripheral faces can also significantly activate the FFA.

Undoubtedly, the dual-task condition is more demanding than either of the two single tasks since subjects have to perform two tasks simultaneously. Therefore, subjects might compensate for this perceived increase in difficulty by a more aroused state resulting in a widespread increase in activity in the dual-task condition. To determine whether this effect accounts for the high level of activity obtained in the dual-task condition, for the trained subjects we looked at activity in the PPA region that had been identified in the localizer runs. This region is more strongly activated by spatial layouts than by faces (Epstein and Kanwisher, 1998). As shown in Fig. 3c, no differential effect was present in the PPA ( $p > 0.05$ ), thus ruling out the possibility that non-specific arousal effects are responsible for the observed results. Likewise, occipital topographic visual areas did not show any differential response to peripherally presented faces (Fig. S2c,  $p > 0.05$ ; 3 trained subjects). Note however, that at the parafoveal topographic location corresponding to the central letter stimulus, early visual cortex BOLD activity remained as strong in the dual-task condition as in the central-task condition (Fig. S2a, b), supporting our assumption that subjects maintained attention to the central letters. In contrast, a strong decrease of BOLD signal in these early areas was observed during the peripheral-task condition when the subjects were not required to attend to the center.

Even for simple tasks such as color or orientation discrimination, achieving good performance in the dual-task paradigm is contingent on substantial training (Braun and Julesz, 1998; Li et al., 2002). We thus wondered whether the high level of activity in the dual-task condition was merely a consequence of training. In other words, can everyone profit from this ability to process faces outside the focus of attention, or is it only acquired after extensive training? Furthermore, since untrained subjects usually show a drop in behavioral performance in the dual-task condition, we were also interested in determining if FFA activity would mirror this decrease. Therefore, in the second experiment, six subjects, untrained in the dual-task condition, performed the experiment in the scanner.

#### *fMRI activity: the role of training*

Six subjects who had never performed in the dual-task condition before (but had been exposed to both single tasks) were tested in the scanner under exactly the same conditions as in the previous experiment. As expected, their behavioral performance on face–gender discrimination dropped considerably when spatial attention was not fully available to the faces: for this group of subjects, average performance in the dual-task condition was  $73.7 \pm 3.0\%$  of performance in the single-task condition (Fig. 2c). On average, the corresponding  $d'$  dropped significantly ( $p < 0.01$ ) from  $1.3 \pm 0.4$  in the single-task to  $0.6 \pm 0.3$  in the dual-task conditions.

Fig. 4 shows the activity in the FFA for these six subjects. As in the data for Fig. 3, a significant effect of the attentional condition on the BOLD signal was observed [ $F(2,15) = 9.46$ ,  $p = 0.002$ ], and a

post-hoc multiple comparisons test revealed that activity in the dual-task and peripheral-task conditions was similar, and a significant reduction was only observed in the central-task condition ( $p < 0.05$ ). Thus, despite the substantial drop in behavioral performance in the dual-task condition, the corresponding BOLD activity did not decrease compared to the single-task level. This implies that training is not a necessary condition for maintaining high levels of FFA activity in the absence of focal attention.

#### *Correlating behavioral performance and the BOLD signal*

The data presented thus far reveal that there does not appear to be a correlation between the amount of BOLD activity in the FFA and the behavioral performance of subjects on gender discrimination. We have observed that although there was a significant reduction in performance for the untrained group of subjects compared to the trained subjects, the levels of BOLD activation were not significantly different. To determine whether there was a correlation on a block-by-block basis between the BOLD activity and behavioral performance for each subject, we correlated performance levels with the percent signal change for each of our subjects on every face-task block. The correlation values thus obtained for each subject were very small ( $r^2 = 0.001$  on average and  $r^2 < 0.12$  in all cases). We also computed the correlation between FFA BOLD activity and behavioral performance over the two groups of trained and untrained subjects. The correlation coefficients ( $r^2$ ) between the average FFA BOLD activity of a subject and his/her average face-task performance (averaged over all face-task blocks) were 0.04 and 0.08 for the six trained and six untrained subjects respectively. These low correlation values suggest that FFA activity (although probably necessary) is not sufficient for good behavioral performance in our face–gender discrimination task.

#### *Whole brain group analysis*

The results in the PPA showed that the effects observed in the FFA were not due to general arousal. However to examine whether other high level visual areas involved in object recognition showed similar effects a whole brain analysis was performed over the group of trained subjects. Specifically we looked in the ventral–occipital complex, and in the region of the lateral occipital complex but did not observe the same pattern of results as in the FFA.

A random effects whole brain analysis did reveal significantly higher activation in the region of the right inferior parietal lobule (Talairach coordinates: 30,  $-48$ , 34;  $p < 0.01$ ) in the dual-task condition, when subjects performed two tasks simultaneously, compared to either of the single-task conditions. This effect of task demands is consistent with the role of parietal regions in attentional control (Culham and Kanwisher, 2001; Corbetta and Shulman, 2002; Behrmann et al., 2004).

## **Discussion**

Our results demonstrate a dissociation between the effects of focal, spatial attention and top–down task-based attention in the FFA. Manipulating the spatial focus of attention alone did not significantly affect the BOLD signal in the FFA as long as the face stimuli remained relevant to the task at hand. These results are compatible with evidence from patients with hemifield neglect

showing that when subjects perform a task on faces presented in the neglected hemifield (i.e. independently of spatial attention), BOLD activity selective for the face stimuli is observed in the FFA (Rees et al., 2000; Vuilleumier et al., 2001a,b). Note that although we consider the task-based component to be non-spatial (based on the assumption of a unique spatial focus of attention (Posner et al., 1980)), this claim is not crucial to our results.

However, at first glance, our result may appear to be at odds with a number of other fMRI studies which have reported a significant decrease in FFA BOLD activity as a result of the attentional manipulation of faces (Wojciulik et al., 1998; O'Craven et al., 1999; Vuilleumier et al., 2001a,b; Pessoa et al., 2002). In fact, the two experimental conditions measured in most of these studies roughly correspond to our peripheral and central-task conditions: subjects either perform a task involving the faces or ignore them completely. And, in agreement with previous findings, we observed significantly distinct levels of BOLD activity between these two conditions. However, by further introducing a third condition in our paradigm (the dual-task condition), we were able to separate the effects of two factors (spatial attention and a task-based form of attention) which might have been confounded in previous reports. Our data show that these factors indeed have distinct effects on the BOLD signal in the FFA. Thus, rather than being at variance with previous reports, these results, together with earlier findings, reveal a more complete picture of how focal attention and top-down task-based attention interact in higher levels of visual cortex.

Although we observed that the FFA BOLD activity was primarily dependent on top-down task-based attention, irrespective of the current spatial focus of attention, we do not wish to imply that that this task-based component alone is the dominant factor affecting neuronal responses. As we discussed earlier, several studies have shown the reverse interaction, namely that focusing spatial attention on task-irrelevant stimuli also enhances their representation in cortex (O'Craven et al., 1999; de Fockert et al., 2001; Downing et al., 2001). Indirect evidence also comes from studies in which manipulating the attentional load results in a significant modulation of BOLD activity in response to task-irrelevant stimuli, in several brain areas (Rees et al., 1997; O'Connor et al., 2002; Pinsk et al., 2004; Yi et al., 2004). Thus, focal attention and the task-based component of attention could have interchangeable effects on brain activity, and it remains to be seen how these effects add up and/or interact in visual cortex (see for example, Treue and Martinez Trujillo, 1999).

It could be argued that the paradigm we use is inadequate in preventing shifts of focal attention to the face stimuli under the dual-task condition. While this possibility cannot be ruled out, the same procedure has been shown to be effective in preventing the discrimination of peripherally presented rotated letters ('T' versus 'L'), an isolated red-green disk from a green-red one, and also the discrimination of higher level stimuli such as inverted faces (Lee et al., 1999; Li et al., 2002; Reddy et al., 2004). Thus the central letter discrimination task does appear to be effective at engaging some attentional resource at the center of the screen—a resource that we have operationally defined as focal, spatial attention.

What is the specific role of training in our paradigm? Our data show that, for both groups of subjects, comparable average levels of FFA activity are obtained in the dual- and peripheral-task conditions. Furthermore, for both groups of subjects, this level of BOLD activity was paired with good behavioral performance, at least in the peripheral-task condition. However, in the dual-task condition, the

same level of FFA BOLD activity only seemed to benefit the trained subjects. Thus, it appears that although information from the BOLD signal was similarly available to both sets of subjects, only the trained subjects were able to use it effectively. Therefore, rather than increasing brain activity in the FFA, training seems to facilitate a more efficient use of the relevant activity, possibly by minimizing competitive bottlenecks that arise (at stages later than the FFA) from processing two tasks simultaneously (Allport, 1980; Duncan, 1980; Pashler, 1984, 1994).

It has been previously reported that the fMRI signal correlates with behavioral performance during object recognition tasks (Grill-Spector et al., 2000; Bar et al., 2001). However our data reveal that for our subjects there is no apparent correlation between behavioral performance and BOLD activity in the FFA. This lack of correlation between FFA BOLD signals and behavioral performance in our data is consistent with recent findings in congenital prosopagnosics who show normal activation in the FFA in response to faces but are remarkably impaired at face processing at the behavioral level (Avidan, 2005). However, one possible difference from earlier studies (Grill-Spector et al., 2000; Bar et al., 2001) lies in the procedure used to modulate performance. These studies used backward masking with very short SOAs to limit stimulus visibility. It is possible that the attentional manipulation in our paradigm limited discriminability (and thus behavioral performance) without affecting the visibility of the faces. When male faces are confused with female faces (and vice versa) at the same level of visibility, no net difference in FFA activation is expected. On the other hand, it is also possible that behavioral performance would be better correlated with a measure of BOLD activity that gauges the selectivity of the FFA to face stimuli (e.g. the resulting signal from a comparison between faces and objects), rather than with the absolute level of BOLD activity as we have shown here. This measure of selectivity would presumably carry information relevant to the face stimuli and thus more directly influence behavioral performance on the gender discrimination task.

The special status of faces with respect to FFA activation is heavily debated. Although it has been argued that faces preferentially activate this region (Kanwisher et al., 1997; Kanwisher et al., 1999), several studies have also shown that other types of natural stimuli cause significant increases in the BOLD signal (Haxby et al., 2001). Not only the stimulus category, but other factors such as the subject's expertise are thought to play a role (Gauthier et al., 1999; Gauthier et al., 2000). Thus, it is unclear whether the results we observe here are due to the "special" status of faces for the visual system or whether they would generalize to other classes of natural stimuli (e.g. natural scenes containing animals or vehicles) for which high levels of performance have been observed in the near-absence of focal attention (Li et al., 2002; Rousset et al., 2002; Reddy et al., 2004; Rousset et al., 2004a,b; Fei-Fei et al., 2005).

With reference to electrophysiology studies, our results showing the absence of a significant effect of focal attention on BOLD activity in the FFA might seem to contradict previous reports of strong attentional modulation at the neuronal level (Moran and Desimone, 1985; Spitzer et al., 1988; Reynolds et al., 1999, 2000; Reynolds and Desimone, 2003). However, it is important to note that these observations have generally been made when two competing stimuli (a preferred and a nonpreferred stimulus) are placed within the receptive field (RF) of a recorded neuron. When a single stimulus is placed within the RF (in the absence of competition), the effect of shifting attention in and out

of the RF is much less pronounced, at least for well-contrasted stimuli (Moran and Desimone, 1985; Haenny et al., 1988; Maunsell et al., 1991; Motter, 1993; Luck et al., 1997; Reynolds et al., 1999). Attentional effects compatible with these single-cell observations have also been reported in fMRI studies (Kastner et al., 1998). Thus, far from being inconsistent, electrophysiological accounts are compatible with the data we report here—namely that, for well isolated and contrasted stimuli (such as our face stimuli), the effect of removing the focus of attention alone, while keeping task demands comparable, does not result in a substantial drop in neuronal activity. These data, however, do not contradict the possibility that focal attention could have a marked effect on BOLD activity under conditions where the stimuli are degraded or presented in cluttered environments.

In conclusion, our results help explain a puzzling discrepancy observed at the behavioral level: in some cases, visual processing can fail dramatically in the absence of attention (e.g. change blindness or inattention blindness (Rock et al., 1992; Simons and Levin, 1997)) while in other cases (dual-task), perception in the near-absence of spatial attention can be quite successful. When visual stimuli or changes are totally unexpected, absence of top-down task-based attention might decrease their associated neuronal representations, as shown here for the FFA. On the other hand, as soon as the range of possible relevant events can be constrained by top-down influence (as in dual-task), neural activities need not suffer even in the near-absence of focal attention.

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#### Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.neuroimage.2007.08.006](https://doi.org/10.1016/j.neuroimage.2007.08.006).

#### References

- Allport, D.A., 1980. Attention and performance. In: Claxton, G. (Ed.), *Cognitive Psychology: New Directions*. Routledge & Kegan Paul, London, pp. 43–67.
- Avidan, G., Hasson, U., Malach, R., Behrmann, M., 2005. Detailed exploration of face-related processing in congenital prosopagnosia: 2. Functional neuroimaging findings. *J. Cogn. Neurosci.* 17, 1150–1167.
- Bar, M., Tootell, R.B., Schacter, D.L., Greve, D.N., Fischl, B., Mendola, J.D., et al., 2001. Cortical mechanisms specific to explicit visual object recognition. *Neuron* 29 (2), 529–535.
- Behrmann, M., Geng, J.J., Shomstein, S., 2004. Parietal cortex and attention. *Curr. Opin. Neurobiol.* 14 (2), 212–217.
- Braun, J., Julesz, B., 1998. Withdrawing attention at little or no cost: detection and discrimination tasks. *Percept. Psychophys.* 60 (1), 1–23.
- Braun, J., Sagi, D., 1990. Vision outside the focus of attention. *Percept. Psychophys.* 48 (1), 45–58.
- Corbetta, M., Shulman, G.L., 2002. Control of goal-directed and stimulus-driven attention in the brain. *Nat. Rev., Neurosci.* 3 (3), 201–215.
- Culham, J.C., Kanwisher, N.G., 2001. Neuroimaging of cognitive functions in human parietal cortex. *Curr. Opin. Neurobiol.* 11 (2), 157–163.
- de Fockert, J.W., Rees, G., Frith, C.D., Lavie, N., 2001. The role of working memory in visual selective attention. *Science* 291 (5509), 1803–1806.
- Downing, P., Liu, J., Kanwisher, N., 2001. Testing cognitive models of visual attention with fmri and meg. *Neuropsychologia* 39 (12), 1329–1342.
- Duncan, J., 1980. The locus of interference in the perception of simultaneous stimuli. *Psychol. Rev.* 87 (3), 272–300.
- Engel, S.A., Glover, G.H., Wandell, B.A., 1997. Retinotopic organization in human visual cortex and the spatial precision of functional mri. *Cereb. Cortex* 7 (2), 181–192.
- Epstein, R., Kanwisher, N., 1998. A cortical representation of the local visual environment. *Nature* 392 (6676), 598–601.
- Epstein, R., Graham, K.S., Downing, P.E., 2003. Viewpoint-specific scene representations in human parahippocampal cortex. *Neuron* 37 (5), 865–876.
- Fei-Fei, L., VanRullen, R., Koch, C., Perona, P., 2005. Why does natural scene categorization require little attention? *Vis. Cogn.* 12 (6), 893–924.
- Gauthier, I., Tarr, M.J., Anderson, A.W., Skudlarski, P., Gore, J.C., 1999. Activation of the middle fusiform ‘face area’ increases with expertise in recognizing novel objects. *Nat. Neurosci.* 2 (6), 568–573.
- Gauthier, I., Skudlarski, P., Gore, J.C., Anderson, A.W., 2000. Expertise for cars and birds recruits brain areas involved in face recognition. *Nat. Neurosci.* 3 (2), 191–197.
- Grill-Spector, K., Kushnir, T., Hendler, T., Malach, R., 2000. The dynamics of object-selective activation correlate with recognition performance in humans. *Nat. Neurosci.* 3 (8), 837–843.
- Haenny, P.E., Maunsell, J.H., Schiller, P.H., 1988. State dependent activity in monkey visual cortex. II. Retinal and extraretinal factors in v4. *Exp. Brain Res.* 69 (2), 245–259.
- Hasson, U., Harel, M., Levy, I., Malach, R., 2003. Large-scale mirror-symmetry organization of human occipito-temporal object areas. *Neuron* 37 (6), 1027–1041.
- Haxby, J.V., Gobbini, M.I., Furey, M.L., Ishai, A., Schouten, J.L., Pietrini, P., 2001. Distributed and overlapping representations of faces and objects in ventral temporal cortex. *Science* 293 (5539), 2425–2430.
- Jenkinson, M., Bannister, P., Brady, M., Smith, S., 2002. Improved optimization for the robust and accurate linear registration and motion correction of brain images. *NeuroImage* 17 (2), 825–841.
- Kanwisher, N., McDermott, J., Chun, M.M., 1997. The fusiform face area: a module in human extrastriate cortex specialized for face perception. *J. Neurosci.* 17 (11), 4302–4311.
- Kanwisher, N., Stanley, D., Harris, A., 1999. The fusiform face area is selective for faces not animals. *NeuroReport* 10 (1), 183–187.
- Kastner, S., De Weerd, P., Desimone, R., Ungerleider, L.G., 1998. Mechanisms of directed attention in the human extrastriate cortex as revealed by functional mri. *Science* 282 (5386), 108–111.
- Lee, D.K., Koch, C., Braun, J., 1999. Attentional capacity is undifferentiated: concurrent discrimination of form, color, and motion. *Percept. Psychophys.* 61 (7), 1241–1255.
- Levy, I., Hasson, U., Avidan, G., Hendler, T., Malach, R., 2001. Center-periphery organization of human object areas. *Nat. Neurosci.* 4 (5), 533–539.
- Li, F.F., VanRullen, R., Koch, C., Perona, P., 2002. Rapid natural scene categorization in the near absence of attention. *Proc. Natl. Acad. Sci. U. S. A.* 99 (14), 9596–9601.
- Luck, S.J., Chelazzi, L., Hillyard, S.A., Desimone, R., 1997. Neural mechanisms of spatial selective attention in areas v1, v2, and v4 of macaque visual cortex. *J. Neurophysiol.* 77 (1), 24–42.
- Malach, R., Levy, I., Hasson, U., 2002. The topography of high-order human object areas. *Trends Cogn. Sci.* 6 (4), 176–184.
- Marois, R., Yi, D.J., Chun, M.M., 2004. The neural fate of consciously perceived and missed events in the attentional blink. *Neuron* 41 (3), 465–472.

- Maunsell, J.H., Sclar, G., Nealey, T.A., DePriest, D.D., 1991. Extraretinal representations in area v4 in the macaque monkey. *Vis. Neurosci.* 7 (6), 561–573.
- Moran, J., Desimone, R., 1985. Selective attention gates visual processing in the extrastriate cortex. *Science* 229 (4715), 782–784.
- Motter, B.C., 1993. Focal attention produces spatially selective processing in visual cortical areas v1, v2, and v4 in the presence of competing stimuli. *J. Neurophysiol.* 70 (3), 909–919.
- O'Connor, D.H., Fukui, M.M., Pinsk, M.A., Kastner, S., 2002. Attention modulates responses in the human lateral geniculate nucleus. *Nat. Neurosci.* 5 (11), 1203–1209.
- O'Craven, K.M., Downing, P.E., Kanwisher, N., 1999. Fmri evidence for objects as the units of attentional selection. *Nature* 401 (6753), 584–587.
- Pashler, H., 1984. Processing stages in overlapping tasks—evidence for a central bottleneck. *J. Exp. Psychol. Hum. Percept. Perform.* 10 (3), 358–377.
- Pashler, H., 1994. Dual-task interference in simple tasks—data and theory. *Psychol. Bull.* 116 (2), 220–244.
- Pessoa, L., McKenna, M., Gutierrez, E., Ungerleider, L.G., 2002. Neural processing of emotional faces requires attention. *Proc. Natl. Acad. Sci. U. S. A.* 99 (17), 11458–11463.
- Pinsk, M.A., Doniger, G.M., Kastner, S., 2004. Push–pull mechanism of selective attention in human extrastriate cortex. *J. Neurophysiol.* 92 (1), 622–629.
- Posner, M.I., Snyder, C.R., Davidson, B.J., 1980. Attention and the detection of signals. *J. Exp. Psychol.* 109 (2), 160–174.
- Reddy, L., Wilken, P., Koch, C., 2004. Face–gender discrimination is possible in the near-absence of attention. *J. Vis.* 4 (2), 106–117.
- Rees, G., Frith, C.D., Lavie, N., 1997. Modulating irrelevant motion perception by varying attentional load in an unrelated task. *Science* 278 (5343), 1616–1619.
- Rees, G., Wojciulik, E., Clarke, K., Husain, M., Frith, C., Driver, J., 2000. Unconscious activation of visual cortex in the damaged right hemisphere of a parietal patient with extinction. *Brain* 123 (Pt 8), 1624–1633.
- Reynolds, J.H., Desimone, R., 2003. Interacting roles of attention and visual salience in v4. *Neuron* 37 (5), 853–863.
- Reynolds, J.H., Chelazzi, L., Desimone, R., 1999. Competitive mechanisms subserve attention in macaque areas v2 and v4. *J. Neurosci.* 19 (5), 1736–1753.
- Reynolds, J.H., Pasternak, T., Desimone, R., 2000. Attention increases sensitivity of v4 neurons. *Neuron* 26 (3), 703–714.
- Rock, I., Linnett, C.M., Grant, P., Mack, A., 1992. Perception without attention: results of a new method. *Cogn. Psychol.* 24 (4), 502–534.
- Rousselet, G.A., Fabre-Thorpe, M., Thorpe, S.J., 2002. Parallel processing in high-level categorization of natural images. *Nat. Neurosci.* 5 (7), 629–630.
- Rousselet, G.A., Thorpe, S.J., Fabre-Thorpe, M., 2004a. How parallel is visual processing in the ventral pathway? *Trends Cogn. Sci.* 8 (8), 363–370.
- Rousselet, G.A., Thorpe, S.J., Fabre-Thorpe, M., 2004b. Processing of one, two or four natural scenes in humans: the limits of parallelism. *Vision Res.* 44 (9), 877–894.
- Simons, D.J., Levin, D.T., 1997. Change blindness. *Trends Cogn. Sci.* 1 (7), 261–267.
- Sperling, G., Melchner, M.J., 1978. The attention operating characteristic: examples from visual search. *Science* 202 (4365), 315–318.
- Spitzer, H., Desimone, R., Moran, J., 1988. Increased attention enhances both behavioral and neuronal performance. *Science* 240 (4850), 338–340.
- Thesen, S., Heid, O., Mueller, E., Schad, L.R., 2000. Prospective acquisition correction for head motion with image-based tracking for real-time fmri. *Magn. Reson. Med.* 44 (3), 457–465.
- Treue, S., Martinez Trujillo, J.C., 1999. Feature-based attention influences motion processing gain in macaque visual cortex. *Nature* 399 (6736), 575–579.
- Vuilleumier, P., Armony, J.L., Driver, J., Dolan, R.J., 2001a. Effects of attention and emotion on face processing in the human brain: an event-related fmri study. *Neuron* 30 (3), 829–841.
- Vuilleumier, P., Sagiv, N., Hazeltine, E., Poldrack, R.A., Swick, D., Rafal, R.D., et al., 2001b. Neural fate of seen and unseen faces in visuospatial neglect: a combined event-related functional mri and event-related potential study. *Proc. Natl. Acad. Sci. U. S. A.* 98 (6), 3495–3500.
- Wojciulik, E., Kanwisher, N., Driver, J., 1998. Covert visual attention modulates face-specific activity in the human fusiform gyrus: Fmri study. *J. Neurophysiol.* 79 (3), 1574–1578.
- Yi, D.J., Woodman, G.F., Widders, D., Marois, R., Chun, M.M., 2004. Neural fate of ignored stimuli: dissociable effects of perceptual and working memory load. *Nat. Neurosci.* 7 (9), 992–996.