Published in final edited form as:
Neuropsychologia. 2008 ; 46(4): 1032–1040.

Voluntary and Involuntary Attention Affect Face Discrimination Differently

Michael Esterman[1,2], **William Prinzmetal**[2], **Joe DeGutis**[2], **Ayelet Landau**[2], **Eliot Hazeltine**[3], **Timothy Verstynen**[4], and **Lynn Robertson**[2,5]

1*Department of Psychological and Brain Sciences, Johns Hopkins University, Baltimore, MD 21218*

2*Department of Psychology, University of California, Berkeley CA 94720*

3*Department of Psychology, University of Iowa, Iowa City, IA 52242*

4*Keck Center for Integrative Neuroscience, University of California, San Francisco, CA 94143*

5*Veterans Administration, Martinez, CA 94553*

Abstract

Do voluntary (endogenous) and involuntary (exogenous) attention have the same perceptual consequences? Here we used fMRI to examine activity in the fusiform face area (FFA-a region in ventral visual cortex responsive to faces) and frontal-parietal areas (dorsal regions involved in spatial attention) under voluntary and involuntary spatial cueing conditions. The trial and stimulus parameters were identical for both cueing conditions. However, the cue predicted the location of an upcoming target face in the voluntary condition but was nonpredictive in the involuntary condition. The predictable cue-condition led to increased activity in the FFA compared to the nonpredictable cue-condition. These results show that voluntary attention leads to more activity in areas of the brain associated with face processing than involuntary attention, and they are consistent with differential behavioral effects of attention on recognition-related processes.

Keywords

FFA; exogenous attention; endogenous attention; fMRI; spatial cueing

Visual attention can be attracted to a location by a sudden onset but it can also be voluntarily moved to a location in anticipation of an upcoming target (Posner, 1980; Posner, Nissen, & Ogden, 1978; Posner, Snyder, & Davidson, 1980). These two forms of spatially orienting attention are also called exogenous and endogenous attention, respectively (Posner, 1978). It is generally proposed that this distinction refers to differences in the control of spatial attention. For example, evidence suggests that involuntary attention is automatic and transient, whereas voluntary attention can be sustained (Nakayama & Mackeben, 1989). It is often assumed that the two forms of attention enhance perceptual processing in the same way and are controlled by the same neural mechanisms (see Gazzaniga, Ivry, & Mangun, 1998).

Send Correspondence to: Michael Esterman, Department of Psychological and Brain Sciences, Johns Hopkins University, 3400 N. Charles St., Baltimore, MD 21218-2686, Email: esterman@jhu.edu, Phone: 510 642-6266.

Recent behavioral data challenge this assumption (Prinzmetal, McCool, & Park, 2005; Prinzmetal, Park, & Garette, 2005). Using a spatial cueing paradigm, they found that both voluntary and involuntary attention affected reaction time similarly. Participants were faster when the target appeared in the cued location (“valid” trials) than in an uncued location (“invalid” trials), as would be expected if both types of attention affected processing in the same way. However, when accuracy was the dependent variable, participants were more accurate when the target appeared at the cued location than at the uncued location only under voluntary attention conditions (Prinzmetal, McCool et al., 2005; Prinzmetal, Park et al., 2005). Furthermore, increasing perceptual difficulty of the target had differential effects on voluntary and involuntary attention (Prinzmetal, Zvinyatskovskiy, & Dilem, 2004). Together, these studies suggest these two types of spatial attention have different perceptual consequences.

Here we examine the neural consequences of the two modes of spatial attention in a face discrimination task and focused primarily on activity in the fusiform face area (FFA) of the ventral processing stream (Allison et al., 1994; Kanwisher, McDermott, & Chun, 1997; Puce, Allison, Gore, & McCarthy, 1995; Sergent, Ohta, & MacDonald, 1992) under voluntary and involuntary conditions. It is well established that the FFA responds to faces more when attention is directed to faces as compared to places or other object categories (Serences, Schwarzbach, Courtney, Golay, & Yantis, 2004; O’Craven, Downing, & Kanwisher, 1999; Wojciulik, Kanwisher, & Driver, 1998). In other words, voluntary object-based attention increases FFA activity. It has also been shown that there is increased FFA activity when spatial attention is directed to a location containing a task-irrelevant face (Downing, Liu, & Kanwisher, 2001). However, to our knowledge, voluntary and involuntary spatial attention effects on FFA responses have not been investigated or compared directly under similar experimental conditions. In the present study, we combine spatial cueing methods with a face discrimination task employing predictable and unpredictable peripheral cueing conditions to determine whether the neural response in the FFA differs under voluntary and involuntary attention conditions. To manipulate whether voluntary or involuntary attention is brought to bear, the probability of a target face appearing at a cued location is varied, while all other aspects of the task are kept constant.

Several studies have used fMRI to compare voluntary and involuntary attention (Kim et al., 1999; Kincade, Abrams, Astafiev, Shulman, & Corbetta, 2005; Mayer, Dorflinger, Rao, & Seidenberg, 2004; Peelen, Heslenfeld, & Theeuwes, 2004; Rosen et al., 1999). Three of these studies found little or no differences between voluntary and involuntary conditions (Kim et al., 1999; Peelen et al., 2004; Rosen et al., 1999). Two studies found differences in parietal-frontal networks that probably mediate the control of attention (Kincade et al., 2005; Mayer et al., 2004). However, none of these studies focused on differences in ventral areas responsible for object recognition. Thus, these studies do not differentiate between potentially distinct neural consequences of the two forms of attention. In the present paper, we exploit the well-established properties of the FFA to examine the consequences of attention in a cortical area related to face recognition.

Importantly, the previous studies compared peripheral cues in involuntary conditions to central cues in voluntary conditions, often with different timing parameters. Under these circumstances, different sensory input between the two conditions cannot be ruled out as the cause of the differences. In contrast, the trial events for the two attention conditions were identical in the present study (Figure 1). Every trial began with a fixation point and two peripheral achromatic rectangles. A spatial cue was presented by having one of the rectangles turn red. At cue offset, a target face briefly appeared in either the cued location (valid trial) or in the uncued location (invalid trial). In the involuntary condition, the cue was not predictive of target location (Jonides, 1980,1981): The target appeared at the cued location on 50% of the trials and at the uncued location on 50% of the trials. In the voluntary condition the cue was predictive of target location: The target appeared at the cued location on 75% of the trials and at the uncued location on 25% of the trials.

The predictive cue summons voluntary attention in that the participant is instructed to use that cue to anticipate the location of the target. The nonpredictive cue manipulates involuntary attention in that participants are told to ignore these cues as they do not carry information about target location. In this way predictive and nonpredictive cue conditions are used as operational variables for voluntary and involuntary attention. Note that using a peripheral cue means that our predictive session has an involuntary component as well. Furthermore, the nature of the task determines that upon target appearance, the participants are required to voluntarily attend to the target location regardless of cue condition.

A critical feature of our design is that the stimulus displays and timing were identical for voluntary and involuntary attention conditions. Thus, the temporal parameters had to be carefully selected. A short period of time between the cue and target favors a larger involuntary attention effect, whereas a long period favors a larger voluntary attention effect (Posner, Cohen, & Rafal, 1982; Warner, Juola, & Koshino, 1990). Fortunately, with a discrimination task (as opposed to detection task), the time between the cue and target can be as long as 400 ms without diminishing the effect of involuntary attention (Lupianez, Milan, Tornay, Madrid, & Tudela, 1997). On the basis of pilot work with these stimuli, we chose a cue-stimulus interval that would give us approximately equivalent voluntary and involuntary attention effects on reaction time (RT).

To preview our results, we find that voluntary attention increases FFA responses when the face appears at the cued location as compared to when it appears at the uncued location. However, this difference is absent with involuntary attention. These findings support the hypothesis that attentional mechanisms involved in voluntary and involuntary attention can have different consequences on ventral, recognition-related cortical functions.

There has been considerable controversy in the literature about whether involuntary attention affects the perceptual representation. As mentioned above, Prinzmetal and his colleagues have found that voluntary attention, but not involuntary attention, influenced accuracy on discrimination tasks (Prinzmetal, McCool et al., 2005; Prinzmetal, Park et al., 2005). On the other hand, Carrasco and her colleagues have found several cases where “exogenous” attention affects accuracy. For example, Cameron, Tai, and Carrasco (2002) and Carrasco, Penpeci-Talgar, and Eckstein (2000) compared a 100% predictive cue with a neutral cue and found higher accuracy with the 100% predictive cue. They interpreted the results as reflecting exogenous attention because they used peripheral cues and relatively short SOAs (<120 ms) [1]. Thus there are cases where involuntary attention may affect accuracy and other where is does not. Because of this, we also conducted a behavioral experiment, the goal of which was to determine which pattern of accuracy we would obtain when the same stimuli used in the fMRI experiment were made difficult to discriminate. We found that involuntary attention did not affect accuracy using faces that were difficult to discriminate with otherwise the identical parameters used in the fMRI experiment. Conversely, voluntary attention did improve discrimination performance. Later we will suggest one possible explanation of why some researchers find effects of involuntary attention on accuracy and others do not.

---

[1] Warner et al. (1990) found that the SOA where voluntary attention began to become effective depended on the level of practice of the observer. The more practice that observers had, the shorter the critical SOA for voluntary attention, as short as 50 ms. Thus the results of Carrasco et al. (2000, 2002) may have reflected voluntary attention.

Materials and Methods

Participants

Ten healthy undergraduate and graduate students at UC Berkeley participated in the fMRI study. Another 32 healthy undergraduate students at UC Berkeley participated in the behavioral study. All had normal or corrected-to-normal vision and ages ranging from 18-30. All the fMRI participants were right handed. All provided informed consent as approved by the UC Berkeley IRB committee.

Behavioral procedure

The target stimuli were created from digital photographs of two males who were similar in appearance (see Figure 1). One of the 2 faces appeared as a target on every trial. Before the target appeared, two boxes were present, and one turned red for 300 ms, directly followed by the face target either in the cued location (“valid” trials) or in the uncued location (“invalid” trials). Participants were instructed to decide which of the two faces was present on each trial. For the predictive cueing condition, 75% of trials were valid, and 25% were invalid, and participants were told that the face usually appeared at the cued location, so it was beneficial to attend to that location. For the nonpredictive cueing condition, 50% of trials were valid and 50% were invalid, and participants were told that the cue was irrelevant, so they should ignore it. Faces were presented for 150 ms. Eye movements were monitored, and trials on which they occurred were eliminated from analysis[2].

For the imaging experiment and the preceding training session, we chose to conduct a version that emphasized RT over accuracy. In this version, the faces were only slightly morphed, so that discrimination was over 90%. Participants were urged to respond as quickly as possible. We used the easier RT version in the scanner because we wanted to control for extraneous neural responses due to differences in guessing, certainty, or accuracy, and focus only on differences in attention. For the behavioral study, faces were morphed such that participants were only 75-80% correct, and accuracy was stressed rather than RT.

Simulated scanner procedure

Scanning sessions were preceded by a practice session in a simulated scanner the day before. In the simulated scanner, participants laid on their back with mirror glasses that enabled them to see the projected screen presentation. Eye movements were monitored with feedback using an Applied Science Laboratory (ASL) eye tracking system. This session allowed participants to practice the task and learn to maintain fixation. By the final block of practice, eye movements were less than 2%, and discrimination accuracy was better than 90% for all participants. During the simulated scanner session, participants performed the same number of blocks/trials they would receive in the scanner (see fMRI procedure below). The order of voluntary and involuntary blocks was counterbalanced between participants.

fMRI procedure

Participants were scanned using a 4 Tesla Varian Scanner at UC Berkeley. Functional images were acquired using a gradient echoplanar sequence (TR = 2000 ms, TE = 28 ms, matrix size = 64 × 64, FOV = 22.4 cm, 3.5 × 3.5 × 5.5 mm voxel size) sensitive to BOLD contrast. Each functional volume consisted of 18 × 5 mm thick axial slices with 0.5 mm gaps between each slice, providing whole brain coverage. Images were projected onto a custom screen mounted at the participant’s chest level and viewed via an angled mirror placed inside the head coil. Responses were made by the right hand using a hand-held fiber optic button box.

---

[2] This paradigm was similar to Prinzmetal, McCool, et al. (2005) Experiments 9-11, but used a different cue-target interval (SOA).

Cueing Task—Each participant performed 6 blocks of the cueing task: 3 consecutive blocks with a predictive cue, and 3 consecutive blocks with a nonpredictive cue. Predictive/nonpredictive order was counterbalanced. Before each block, participants were reminded of the cue predictability (i.e., whether to ignore the cue or not) and to maintain fixation. Each block consisted of 64 trials. ITI was jittered: 25% were 8 sec, 25% were 6 sec, and 50% were 4 sec.

FFA Localizer—Between the predictive and nonpredictive blocks of the main experiment, each participant performed a FFA localizer task with a standard procedure (Kanwisher et al., 1997), previously used for ROI definition to explore attention effects of lateralized faces (e.g. Wojciulik et al., 1998). The faces in the localizer task were presented at fixation and were different in identity and size (larger) than the faces used in the subsequent cueing task. They were shown 16-second blocks consisting of either faces, scenes, or fixation. In each block, 20 images were presented for 500 ms each with 300 ms ISI. Participants were instructed to press the response pad when the current image was the same as the image immediately preceding it (on average, one response was required for each block of images). There were 7 blocks of each type, and the scan lasted 5 minutes and 20 seconds. Face selective regions were derived from contrasting face and scene blocks in this one-back task.

fMRI Data Analysis

Initial data preparation included image reconstruction, motion correction using a six-parameter, rigid-body, least-squares alignment, and spatial smoothing (8-mm FWHM Gaussian kernel). SPM2 was used for all processing and analyses (Wellcome Institute of Cognitive Neurology, London, UK).

FFA Localizer—For each participant, the FFA was defined as the peak 15 voxels which included the maximum peak voxel in the middle fusiform gyrus with greater BOLD signal for faces compared to scenes. This yielded a right and left FFA for 6 participants, a right FFA only for 2 participants, and a left FFA only for 2 participants. For participants with both left and right FFA, twice as much data were available for the ROI analyses.

ROI analysis-native space FFA—BOLD signal corresponding to each trial type was assessed using a finite impulse response (FIR) model. The signal change in BOLD response from baseline (fixation pattern alone) for each time point corresponding to the first 16 time-interpolated TRs (16 seconds) was estimated for each voxel and condition. This technique does not assume a canonical shape of the hemodynamic response function. The response function for each FFA was the average of all voxels in the ROI. Planned comparisons of peak BOLD responses were done on the signal collapsed across 4-6 seconds. The ANOVA was conducted with activation from 1-7 seconds, which corresponded to the time period in which all BOLD responses were greater than zero. Note that these response functions are a result of BOLD responses to both cue and target, since a single trial is modeled as a single event. However, this was the case for both voluntary and involuntary attention conditions. All trials were included in the analyses, included errors, which occurred infrequently (4% of trials), and did not differ between the conditions (see Results).

Whole brain group analysis—In addition to the ROI analysis, a whole brain analysis was conducted. Estimates of task-related effects were obtained using a general linear model which takes into account the intrinsic variance-covariance structure of the time-series (Friston, 1995). Separate parameter estimates were modeled for each condition. These models were generated for each participant in native space. For a given effect of interest, whole-brain contrast maps were determined for each participant. Each participant's T1-weighted high resolution anatomical scan was normalized into the same coordinate frame as the MNI-template brain by using a 7 × 8 × 7 parameter nonlinear transform. The resulting transformation parameters were applied to all contrast images that were generated in native space. Voxel size of the transformed maps was 2 × 2 × 2 mm. Analysis of significance at the group level was determined using a random effects analysis, using a 1-sample t-test or paired t-test on the contrast maps. We calculated a family-wise error corrected threshold of p=0.05, derived from the compiled Family-wise error (FWE) values for all individual subjects in the group. This value corresponds to an uncorrected critical p-value of 0.0007. Thresholded clusters of 10 or more voxels are reported. Whole brain contrasts were done to examine validity effects in the voluntary and involuntary conditions and how they interact, particularly in frontal-parietal areas (Table 1, Figure 3). To examine reorienting after voluntary and involuntary orienting, valid trials were contrasted with invalid trials for each cue type. Validity effects (invalid > valid) isolate activity associated with reorienting when the target appears at the uncued location from the activity associated with orienting to the cue. To compare reorienting between the voluntary and involuntary conditions, validity effects (invalid > valid) were contrasted between predictive and nonpredictive cueing blocks, thus examining the interaction of validity and cue type.

Results

Behavioral results in the scanner

Mean correct RT for each cell of the design for each participant was analyzed by ANOVA for repeated measures. There was a main effect of validity, and no interaction with session. For both predictive and nonpredictive blocks, participants were faster on valid than invalid trials (Predictive: valid=684 ms, invalid= 720 ms; $p<0.05$: Nonpredictive: valid=674 ms, invalid= 711 ms; $p<0.01$), consistent with previous findings (e.g. Prinzmetal et al., 2005a). The magnitude of the validity benefit was similar: 36 ms for voluntary and 37 ms for involuntary attention. There was no effect of order (predictive vs. nonpredictive first) on the magnitude of the cueing effect ($F<1$). Accuracy was high for both types of cues (Predictive: valid=96%, invalid=94%, $p>0.1$; Nonpredictive: valid=97%, invalid=96%, $p>0.1$). With accuracy as the dependent measure, the ANOVA revealed no effects of validity or session, and no interaction.

Imaging Data

FFA Identification—The difference between faces and scenes elicited face-specific activity in the fusiform gyrus for all participants, defining the FFA regions of interest (see Methods section).

ROI analysis-effects of spatial cueing on the FFA—Because only 6 of 10 participants had both a right and left FFA, we had reduced power to investigate differences between left and right FFA. Although right FFA exhibited more task related activity overall, side of FFA did not interact with attention type. A finite impulse response (FIR) model (see Methods) was used to estimate the hemodynamic response for each condition within each participant's FFA (s). These response functions were subjected to an ANOVA with target laterality (contralateral/ipsilateral), cue laterality (contralateral/ipsilateral), attention type (voluntary/involuntary), and time (1 sec through 7 sec) as factors. Overall, there was greater FFA response for contralateral compared to ipsilateral cues and faces (cue laterality × time, $F_{6,54}=2.41$, $p<0.05$; target laterality × time, $F_{6,54}=8.81$, $p<0.01$). These interactions were qualified by higher order interactions with session (predictive vs nonpredictive). Specifically, different consequences of voluntary and involuntary orienting were revealed by a significant 4-way interaction of the FFA response between target laterality, cue laterality, attention type, and time ($F_{6,54}=2.44$, $p<0.05$). To explore the nature of this interaction we analyzed the peak BOLD responses (collapsed across 4-6 seconds) in the FFA for each type of attention.

The key findings are that BOLD response in the contralateral FFA is increased for valid compared to invalid trials, but only when voluntary attention was manipulated. Figure 2 compares valid and invalid trials in the contralateral FFA, for voluntary and involuntary attention. The sample trials in the figures are examples for the right FFA, presented for illustrative purposes. These comparisons represent two ways to describe the validity effects, one focusing on where the target is presented on the two types of trials (valid vs. face contralateral), and the other focusing on where the cue is presented on the two types of trials (valid vs. cue contralateral). Both of these comparisons are of interest, since we cannot discern which part of the trial (cue or target) maximally accounts for effects in the BOLD response. Cues and targets are part of the same event in this fMRI design, and therefore further experimentation using different methods are needed in order to completely separate cue and target processing.

Validity Effect 1: For predictive cuing conditions, when the cue and face both appeared in the same location (Valid trials, Figure 2), contralateral FFA responses were enhanced relative to an uncued face (Invalid trials, face contralateral, Figure 2; $F_{1,54}=7.48$, $p<0.01$). Involuntary attention did not produce differences between these conditions (Figure 2; $F_{1,54}=1.20$, $p>0.2$). Despite the same sensory input, predictive cues modulated FFA activity, while nonpredictive cues did not. When a lateralized face was presented, activity in the contralateral FFA was enhanced by a valid predictive cue. When the face was preceded by a nonpredictive cue, the FFA responded equivalently to a cued and uncued face.

Validity Effect 2: This effect highlights how voluntary and involuntary attention affects the laterality of the FFA response. For predictive cuing conditions, when the cue and face both appeared in the same location (Valid, Figure 2), contralateral FFA responses were enhanced relative to the cue alone at the same location (Invalid, cue contralateral, Figure 2; $F_{1,54}=43.1$, $p<0.001$). Involuntary attention did not produce differences between these conditions (Figure 2; $F_{1,54}=1.45$, $p>0.2$). When a lateralized cue was presented, activity in the contralateral FFA was enhanced when the face appeared in the expected location (with predictive cues). When the cue was not predictive, the FFA response is not modulated by the face location (no lateralized effect of face location).

In sum, when attention was voluntarily deployed to peripheral areas of the visual field, neural activation in the contralateral FFA was greater when the face appeared in the cued location, consistent with increased processing of cues and/or faces in this region compared to cues and/or faces in unattended regions. However, when attention was involuntarily captured, no such enhancement was observed.

We also observed a trend for a main effect of session (Predicitve>Nonpredicitve; $F_{1,9}=3.92$, $p=0.079$). In addition to the validity related attentional modulation reported above, this could represent a sustained attention effect, such as a baseline shift for anticipating the predictive cue. Although there appears to be greater activity in the predictive session, even at time 0 (at the onset of the cue), this effect is not significant ($p>0.1$).

Whole brain analysis—In addition to the primary region of interest (FFA), whole brain analyses were conducted to ascertain brain regions influenced by cue validity in the different attention conditions (Table 1). All reported comparisons are significant at a family-wise error corrected $p<0.05$. By comparing valid trials and invalid trials when the cue was predictive to when the cue was not predictive, we identified regions involved in spatial reorienting of attention after voluntary and involuntary shifts of attention (Table 1; Figure 3a and b). In the voluntary attention condition, regions in the left and right ventral prefrontal cortex, as well as right temporal-parietal junction (TPJ) were significantly more active on invalid compared to valid trials. In contrast, following involuntary orienting, regions in the right superior parietal cortex and left inferior frontal cortex showed more activity associated with reorienting on invalid trials. In addition, the interaction of validity and cue type was examined by comparing validity effects (invalid > valid) between predictive and nonpredictive conditions (Table 1, bottom; Figure 3c). This analysis revealed regions in the temporal-parietal junction (TPJ) bilaterally where activity was greater for reorienting after voluntary shifts of attention to the cue versus involuntary shifts. We also compared nonpredictive valid trials to baseline, in order to determine whether there was any evidence for activity in these TPJ regions associated with involuntary orienting, and found no such activity (even when we reduced the threshold to an uncorrected $p=0.01$).

Behavioral Study

This experiment was conducted to determine whether decreasing discriminability of the faces leads to different effects of voluntary and involuntary attention on accuracy, which served as the main dependent measure. Accuracy was analyzed by mixed ANOVA with attention type (predictive, nonpredictive) and validity (valid, invalid) as factors. There was a significant interaction between cue validity and attention type ($F_{1,30}=4.30$, $p<0.05$; Figure 4), and no main effects of either attention type or validity. Consistent with Prinzmetal et al. (2005a), there was a significant effect of validity with predictive cues (valid=79.6%, invalid=75.9%, $F_{1,30}=4.46$, $p<0.05$) but not with nonpredictive cues (valid=79.2%, invalid=80.7%, $F<1$).

Discussion

Our findings demonstrate that voluntary and involuntary attention can have different neural consequences in areas associated with perceptual processing in the ventral system. FFA activity was modulated when a target face was validly cued, but only under voluntary attention conditions. The results in voluntary attention conditions cannot be accounted for by sensory mechanisms because the sensory events were identical for predictive and nonpredictive conditions. The only difference between voluntary and involuntary conditions was the proportion of valid to invalid trials. With predictive cues, when the face was presented in the cued location, the contralateral FFA response was greater than to the cue alone or face alone. In marked contrast, with irrelevant cues (nonpredictive), responses to co-occurring cues and targets were no greater than responses to contralateral cue or targets alone (Figure 2).

The differences in BOLD response between voluntary and involuntary attention cannot be attributed to factors such as speed of processing or task difficulty, as RTs did not differ across the attention conditions. Interestingly, the pattern of activation in the FFA fits with what we found in our behavioral study. Predictive spatial cues modulated both FFA and accuracy, while nonpredictive cues did not modulate either the FFA or accuracy. Together, the findings suggest a potential mechanism for our behavioral pattern of results, such that the voluntary attention effect in the FFA could be at least partially responsible for better recognition performance when the task is made more difficult. In fact, we predict that if the face discrimination task was harder, we could see larger voluntary attention effects, both behaviorally, and in the FFA. Manipulating perceptual difficulty in an fMRI paradigm will be an important direction for future study.

An alternative explanation for our results is that the lack of enhancement in the involuntary condition could be due to inhibition or suppression of cue processing, rather than an enhancement caused by voluntary attention. Importantly, the experiment is designed such that stimuli are identical in the voluntary and involuntary attention conditions. Therefore attention must be causing the difference between the two conditions, whether it is facilitation or inhibition. The critical elements in interpreting our attention effect are the behavioral data, which demonstrates 1) faster RTs to validly cued faces than invalidly cued faces, even with involuntary attention (i.e., there was no inhibition of return) and 2) better discrimination of faces after voluntary attention rather than suppression after involuntary attention (i.e., worse performance at the cued location). Given these findings, we predicted FFA enhancement after voluntary attention and a reduction or absence of this enhancement following involuntary attention. This correspondence with perceptual performance led to the current interpretation of our imaging results in the FFA.

There are cases in the literature where nonpredictive cues or short SOAs do affect accuracy (e.g., Cameron et al., 2002; Carrasco et al., 2000; Horstmann, 2002; Shiu & Pashler, 1994). One critical difference between those that show an accuracy effect and those that do not is what determines the limits on performance. Performance can be limited because the targets are very similar. Alternatively, performance can be limited by not knowing which location contained the target. In the present experiment (and those of Prinzmetal, McCool et al., 2005) the limit on performance was due to the similarity of the targets - it was quite clear which location contained the target. In other experiments, that found accuracy effects with short SOAs and/or nonpredictive cues the limit on performance may have been on knowing which location contained the target. For example, Cameron, et al. (2002) found that accuracy was affected by a spatial cue with a relative short SOA. Gould, Wolfgang, and Smith (in press; also see Smith, Wolfgang, & Sinclair, 2004) replicated these results, but demonstrated that when the target location was clearly marked by high contrast cross hairs, the effect disappeared.

There are at least two mechanisms whereby location uncertainty could create an accuracy effect. First, an accuracy effect could be mediated at a decision level of analysis. Perceptual information is registered equally at cued and uncued locations, but participants base their responses on the information in the cued location (e.g. Shaw, 1980; Shiu & Pashler, 1994). A second mechanism is a serial search mechanism. Which location contains the target is not immediately apparent, so participants go through a serial search and they are biased to begin this search at the cued location[3]. One might ask whether this directed search (beginning at the cued location) involves the same neural mechanism as voluntary attention. Our fMRI results suggest one method of addressing this question. If we increase the difficulty of knowing which location contains the target, by adding a foil and/or additional locations, would be get FFA modulation even with a nonpredictive cue?

The present study does not examine which visual areas are modulated by involuntary attention. Thus, we only present a single dissociation between voluntary and involuntary attention. However, this is a limitation of the design, since both of our attention conditions contain an involuntary or stimulus-driven component. As such, we are unable to isolate the effects of exogenous attention. Serences et al. (2005) did find effects of involuntary attentional capture on extrastriate cortical activity. However, in that study, attention was drawn to a task irrelevant spatial location with a task relevant target feature. This kind of capture has a top-down component, namely goal directed attention to a relevant feature. Liu, Pestilli, and Carrasco (2005) found increased V4 activity in a nonpredictive cuing situation under conditions when two potential sinusoids appeared as targets after a cue and participants had to select the one with the relevant feature (orientation). Our study differs from this in that the target display was a single item and selection of the target location was relatively easy (i.e., there was very little search or location uncertainty). While our study does not isolate a locus of involuntary attentional selection, we have shown that its consequences differ from voluntary attention in a high-level visual area associated with object recognition. Future studies will be necessary to directly compare these types of spatial attention in various regions of the visual hierarchy. Using peripheral faces in the localizer task is one way to allow functional identification of

---

[3] Smith et al. (2004) proposed a related mechanism. All items are perceived with equal fidelity, but are transferred into a durable visual memory in a serial fashion. The bias is to begin with the cued location so that items in that location are less likely to be disrupted by a subsequent mask.

additional visual regions of interest in order to do similar comparison as presently done in the FFA.

While our study focused on faces and the FFA, we do not believe our voluntary attention effects are unique to this region of cortex. Other studies of ‘pure’ voluntary attention have found attentional modulations throughout the visual hierarchy, such as V2, VP, V4, and TEO (Hopfinger, Buonocore, & Mangun, 2000; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999). Future studies using retinotopic mapping to identify such regions of interest may reveal similar dissociations between voluntary and involuntary attention, but this remains an open question.

As previously noted, fMRI, in principal, does not have the temporal resolution to differentiate cue from target related activity, or even whether the current effects are early and perceptual, or occur after the task or decision process are completed. However, there are now indications, using EEG, that there are differences in gamma band response to voluntary and involuntary spatial attention to faces (Landau, Esterman, Robertson, Bentin, & Prinzmetal, in press). EEG has the temporal resolution to measure cue and face processing separately. Landau et al. finds differences in both cue and target processing between the two types of attention, suggesting that our current findings do reflect differences in task-related stimulus processing.

Our whole brain analyses compared reorienting in voluntary and involuntary conditions and revealed more temporal parietal junction activity (TPJ) associated with reorienting after predictive cues. This finding is partly consistent with other studies demonstrating that the TPJ is associated with target processing when those targets appear at unexpected or unattended locations (Corbetta, Kincade, Ollinger, McAvoy, & Gordon, 2000; Corbetta & Shulman, 2002; Kincade et al., 2005; Serences et al., 2005). While these studies find a right hemisphere lateralized reorienting system, our study indicates that both hemispheres may participate in this function. Importantly, this TPJ activity was not present following a shift of involuntary attention. This finding is similar to of Kincade et al. (2005), which found that activity in the TPJ was associated with reorienting following an endogenous predicitive cue, but not a nonpredicitive peripheral cue. That study also showed that TPJ did not respond to the nonpredictive peripheral cues above a neutral cue condition. Although we were not able to separate cue from target related activity, we did not find any activity in these TPJ regions on nonpredicitive valid trials. Indovina & Macaluso (2007) also found that highly salient, but task irrelevant stimuli did not engage the ventral attention network.

The present study demonstrates that voluntary and involuntary orienting of attention can have different effects on a percept-related cortical area in the ventral stream and are consistent with perceptual enhancement when voluntary attention is employed. The interaction between voluntary and involuntary attention and validity effects is also consistent with behavioral differences between errors and reaction times to valid and invalid cues reported previously in the behavioral literature. Both voluntary and involuntary attention produced faster responses at validly cued locations than invalidly cued locations. However, only voluntary attention increased accuracy in a situation where the limit on performance was not locating the target. Together, these results suggest that neural activity in the FFA reflects distinct changes in processing associated with the two types of attentional orienting.

While both the voluntary and involuntary systems recruit many overlapping regions of frontal and parietal cortex (Kim et al., 1999; Mayer et al., 2004; Peelen et al., 2004; Rosen et al., 1999), the present study indicates that their consequences on perceptual systems in the ventral cortex can in fact differ, both with regard to their effects on neural responses and on performance.

References

Allison T, Ginter H, McCarthy G, Nobre AC, Puce A, Luby M, et al. Face recognition in human extrastriate cortex. Journal of Neurophysiology 1994;71(2):821–825. [PubMed: 8176446]

Cameron EL, Tai JC, Carrasco M. Covert attention affects the psychometric function of contrast sensitivity. Vision Research 2002;42(8):949–967. [PubMed: 11934448]

Carrasco M, Penpeci-Talgar C, Eckstein M. Spatial covert attention increases contrast sensitivity across the CSF: Support for signal enhancement. Vision Research 2000;40:1203–1215. [PubMed: 10788636]

Corbetta M, Kincade JM, Ollinger JM, McAvoy MP, Gordon SL. Voluntary orienting is dissocitated from target detection in human posterior parietal cortex. Nature Neuroscience 2000;3:201–215.

Corbetta M, Shulman GL. Control of goal-directed and stimulus-driven attention in the brain. Nature Reviews Neuroscience 2002;3(3):201–215.

Downing P, Liu J, Kanwisher N. Testing cognitive models of visual attention with fMRI and MEG. Neuropsychologia 2001;39:1329–1342. [PubMed: 11566315]

Friston KJ. Statistical parametric mapping: Ontology and current issues. Journal of Cerebral Blood Flow & Metabolism 1995;15:361–370. [PubMed: 7713993]

Gazzaniga, MS.; Ivry, RB.; Mangun, GR. In Cognitive neuroscience: The biology of the mind. W.W. Norton; New York: 1998. p. 223

Gould IC, Wolfgang BJ, L. SP. Spatial uncertainty explains exogenous and endogenous attentional cuing effects in visual signal detection. Journal of Vision. in press

Hopfinger JB, Buonocore MH, Mangun GR. The neural mechanism of top-down attentional control. Nature Neuroscience 2000;3(3):284–291.

Horstmann G. Evidence for attentional capture by a surprising color singleton in visual search. Psychological Science 2002;13(6):499–505. [PubMed: 12430832]

Indovina I, Macaluso E. Dissociation of stimulus relevance and saliency factors during shifts of visuospatial attention. Cerebral Cortex 2007;17(7):1701–11. [PubMed: 17003078]

Jonides J. Towards a model of the mind's eye's movement. Canadian Journal of Psychology 1980;34:103–112. [PubMed: 7448632]

Jonides, J. Voluntary versus automatic control over the mind's eye's movement. In: Long, JB.; Baddeley, AD., editors. Attention and performance IX. Erlbaum; Hillsdale, NJ: 1981.

Kanwisher N, McDermott J, Chun MM. The fusiform face area: a module in human extrastriate cortex specialized for face perception. Journal of Neuroscience 1997;17(11):4302–4311. [PubMed: 9151747]

Kastner S, Pinsk MA, De Weerd P, Desimone R, Ungerleider LG. Increased activity in human visual cortex during directed attention in the absence of visual stimulation. Neuron 1999;22(4):751–761. [PubMed: 10230795]

Kim YH, Gitelman DR, Nobre AC, Parrish TB, LaBar KS, Mesulam MM. The large-scale neural network for spatial attention displays multifunctional overlap but differential asymmetry. Neuroimage 1999;9(3):269–277. [PubMed: 10075897]

Kincade JM, Abrams RA, Astafiev SV, Shulman GL, Corbetta M. An event-related functional magnetic resonance imaging study of voluntary and stimulus-driven orienting of attention. Journal of Neuroscience 2005;25(18):590–600.

Landau A, Esterman M, Robertson L, Bentin S, Prinzmetal W. Different Effects of Voluntary and Involuntary Attention on EEG Activity in the Gamma Band. Journal of Neuroscience 2007;27:11986–90. [PubMed: 17978039]

Liu T, Pestilli F, Carrasco M. Transient attention enhances perceptual performance and fMRI response in human visual cortex. Neuron 2005;45:469–477. [PubMed: 15694332]

Lupianez J, Milan EG, Tornay FJ, Madrid E, Tudela P. Does IOR occur in discrimination tasks? Yes, it does, but later. Perception & Psychophysics 1997;59(8):1241–1254. [PubMed: 9401458]

Mayer AR, Dorflinger JM, Rao SM, Seidenberg M. Neural networks underlying endogenous and exogenous visual-spatial orienting. Neuroimage 2004;23(2):534–541. [PubMed: 15488402]

Miller E, Cohen J. An integrative theory of prefrontal cortex function. Annual Reviews Neurosicence 2001;24:167–202.

Nakayama K, Mackeben M. Sustained and transient components of focal visual attention. Vision Research 1989;22(10):1261–1271. [PubMed: 7179746]

O'Craven KM, Downing P, Kanwisher N. fMRI evidence for objects as the units of attentional selection. Nature 1999;401:584–587. [PubMed: 10524624]

Peelen MV, Heslenfeld DJ, Theeuwes J. Endogenous and exogenous attention shifts are mediated by the same large-scale neural network. Neuroimage 2004;22(2):822–830. [PubMed: 15193611]

Posner, MI. Chronometric explorations of mind. Erlbaum; Hillsdale, N.J.: 1978.

Posner MI. Orienting of attention. Quarterly Journal of Experimental Psychology 1980;32:3–25. [PubMed: 7367577]

Posner MI, Cohen YA, Rafal RD. Neural systems control of spatial orienting. Philosophical Transactions of the Royal Society B 1982;298:187–198.

Posner, MI.; Nissen, MJ.; Ogden, WC. Attended and unattended processing modes: the role of set for spatial location. In: Pick, HJ.; Saltzman, E., editors. Models of perceiving and processing information. Erlbaum; Hillsdale, NJ: 1978. p. 137-158.

Posner MI, Snyder CRR, Davidson BJ. Attention and the detection of signals. Journal of Experimental Psychology: General 1980;109:160–174.

Prinzmetal W, McCool C, Park S. Attention: reaction time and accuracy reveal different mechanisms. Journal of Experimental Psychology: General 2005;134(1):73–92. [PubMed: 15702964]

Prinzmetal W, Park S, Garette R. Involuntary Attention and Identification Accuracy. Perception & Psychophysics 2005;67:1344–1353. [PubMed: 16555586]

Prinzmetal, W.; Zvinyatskovskiy, A.; Dilem, L. Voluntary and Involuntary Attention Have Different Consequences: The Effect of Perceptual Difficult; Paper presented at the Annual Meeting of the Psychonomic Society; Minneapolis, MN. 2004;

Puce A, Allison T, Gore J, McCarthy G. Face-sensitive regions in human extrastriate cortex studied by functional MRI. Journal of Neurophysiology 1995;74:1192–1199. [PubMed: 7500143]

Rosen AC, Rao SM, Caffarra P, Scaglioni A, Bobholz JA, Woodley SJ, et al. Neural basis of endogenous and exogenous spatial orienting. A functional MRI study. Journal of Cognitive Neuroscience 1999;11(2):135–152. [PubMed: 10198130]

Serences JT, Schwarzbach J, Courtney SM, Golay X, Yantis S. Control of object-based attention in human cortex. Cerebral Cortex 2004;14:1346–1357. [PubMed: 15166105]

Serences JT, Shomstein S, Leber AB, Golay X, Egeth HE, Yantis S. Coordination of voluntary and stimulus-driven attentional control in human cortex. Psychological Science 2005;16:114–122. [PubMed: 15686577]

Sergent J, Ohta S, MacDonald B. Functional neuroanatomy of face and object processing. A positron emission tomography study. Brain 1992;115(1):15–36. [PubMed: 1559150]

Shaw, ML. Identifying attentional and decision-making components in information processing. In: Nickerson, RS., editor. Attention and Performance VIII. Earlbaum; Hillsdale, NJ: 1980. p. 277-296.

Shiu PL, Pashler H. Negligible effect of spatial precuing on identification of single digits. Journal of Experimental Psychology: Human Perception and Performance 1994;20:1037–1054.

Smith PL, Wolfgang BJ, Sinclair AJ. Mask-Dependent Attentional Cuing Effects in Visual Signal Detection: The Psychometric Function for Contrast. Perception & Psychophysics 2004;66(6):1056–1075. [PubMed: 15675651]

Warner CB, Juola J, Koshino H. Voluntary allocation versus automatic capture of visual attention. Perception & Psychophysics 1990;48:243–251. [PubMed: 2216651]

Wojciulik E, Kanwisher N, Driver J. Covert visual attention modulates face-specific activity in the human fusiform gyrus: fMRI study. Journal of Neurophysiology 1998;79(3):1574–1578. [PubMed: 9497433]

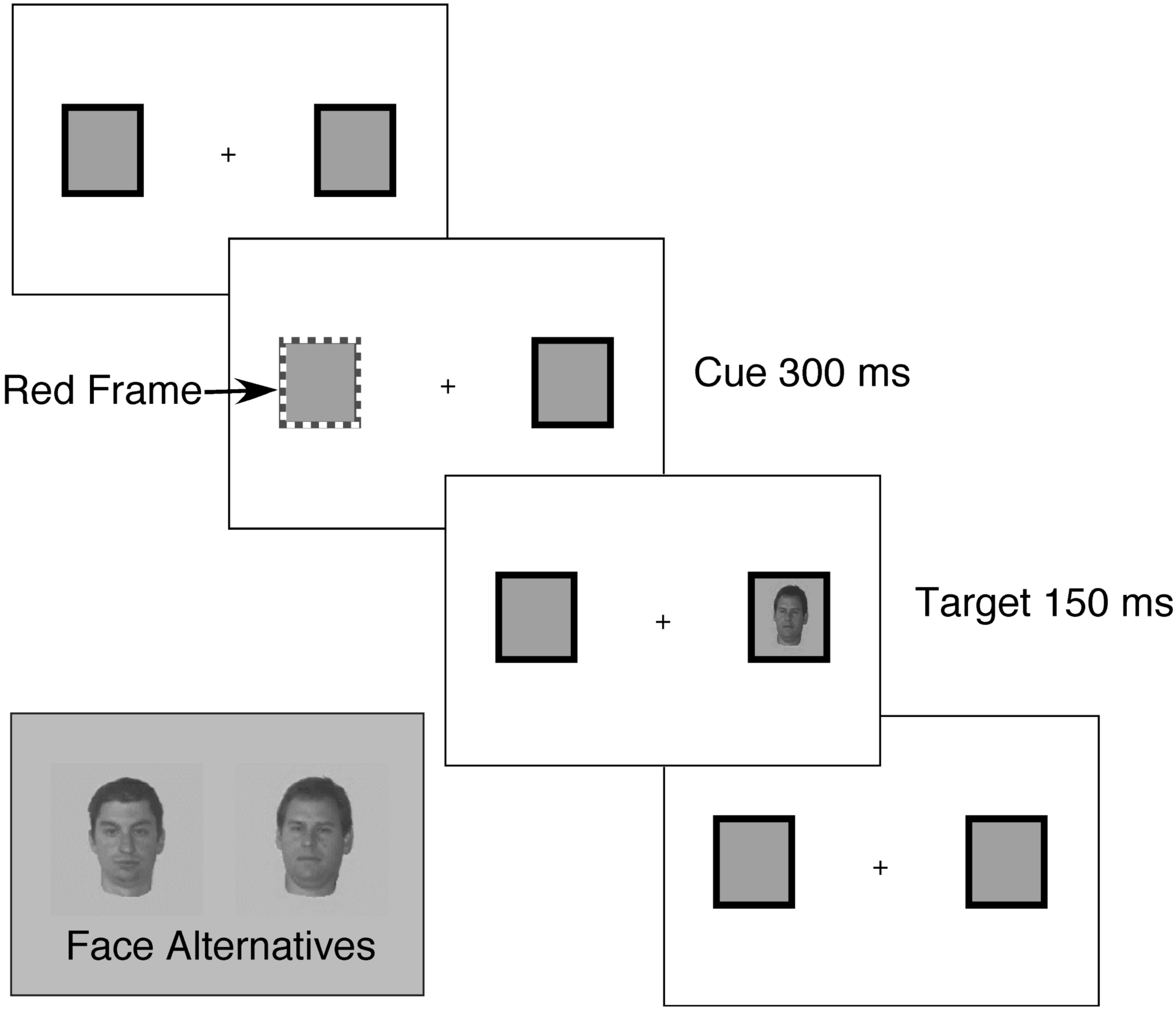

Figure 1.

Spatial cueing procedure. Participants performed a face discrimination task. To examine voluntary and involuntary attention, the cue was either predictive or nonpredictive of a subsequent target face location.

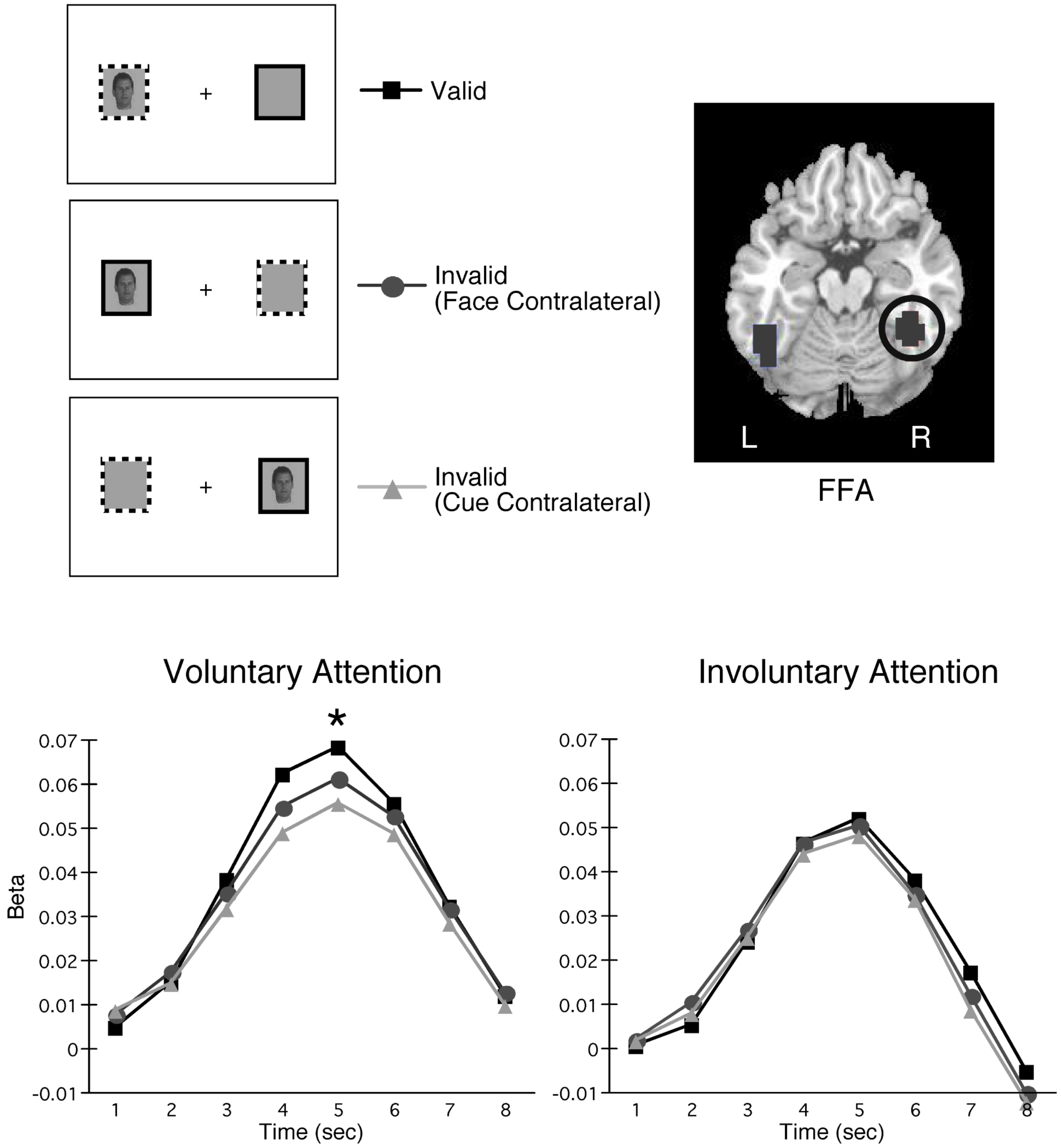

Figure 2.

Validity Effect in the FFA. ROI analysis of FFA, showing evoked blood oxygenation level-dependent (BOLD) time course in the contralateral FFA as a function of type of attention and cue validity. When the face is preceded by a valid spatial cue (valid trials), there is a greater evoked response than to an uncued face (invalid trial, contralateral face), for voluntary attention but not for involuntary attention. Similarly, when the face appears in the cued location (valid trials), there is a greater evoked response than when the face does not appear in the cued location (invalid trials, contralateral cue), but only with voluntary attention and not with involuntary attention. Example contrasts (top-left) are shown for right FFA, however the graphs represent data from both FFAs (for left FFA, the contrast is flipped left-right).

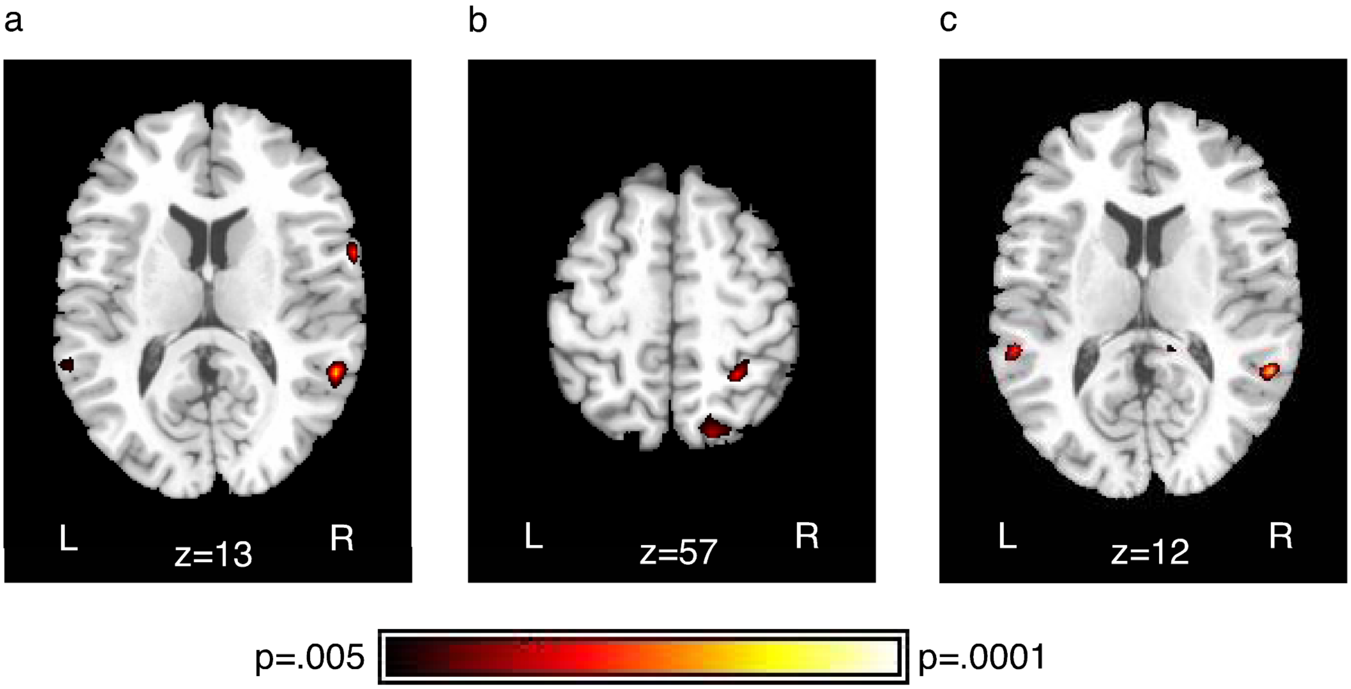

Figure 3.

Group whole brain analyses displaying effects of spatial reorienting of attention (Invalid trials > Valid trials) in the a) voluntary attention condition and b) involuntary attention condition. c) Differences in reorienting between voluntary and involuntary conditions (Predictive Invalid - Valid vs. Nonpredictive Invalid - Valid). P-value range is uncorrected, shown for illustrative purposes (0.0007 corresponds to a Family-wise error (FWE) corrected threshold of p=0.05).

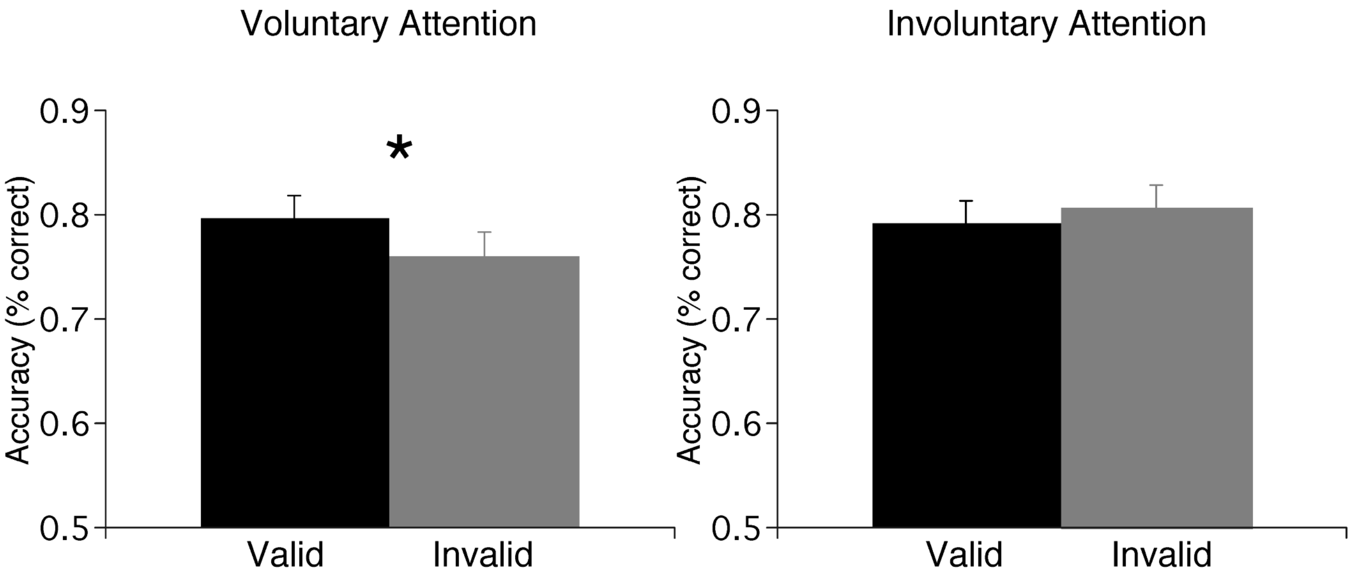

Figure 4.

Results of behavioral experiment, displaying face discrimination accuracy as a function of cue validity and attention conditions.

Table 1

Group whole brain analyses displaying validity effects for voluntary and involuntary attention conditions (reorienting) and differences between these types of attention (Predictive Invalid - Valid > Nonpredictive Invalid - Valid)

Effect Region	**Laterality**	**X**	**Y**	**Z**	**T**	**Voxels**
Reorienting of Attention (Invalid > Valid)						
Voluntary Attention (Predictive Cues)						
Temporal Parietal Junction	R	58	-48	12	8.52	47
Ventral Prefrontal Cortex	R	66	6	14	6.44	10
	L	-44	22	24	5.47	14
Involuntary Attention (Nonpredictive Cues)						
Superior Parietal Lobule	R	26	-50	60	6.85	14
	R	24	-72	50	6.68	51
Dorsal Prefrontal Cortex	L	-32	14	42	6.87	14
Ventral Prefrontal Cortex/Inferior Orbital Frontal	L	-32	24	-8	6.09	12
Voluntary Attention > Involuntary Attention						
Temporal Parietal Junction	L	-58	-38	8	6.49	22
	R	58	-46	14	5.25	12