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From sensory processes to conscious perception

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Abstract

In recent years, cognitive neuroscientists have begun to explore the process of how sensory information gains access to awareness. To further probe this process, event-related functional magnetic resonance imaging (fMRI) was used while testing subjects with a paradigm known as the “attentional blink.” In this paradigm, visually presented information sporadically fails to reach awareness. It was found that the magnitude and time course of activation within the anterior cingulate (BA 32), medial prefrontal cortex (BA 9), and frontopolar cortex (BA 10) predicted whether or not information was consciously perceived during the critical period for the attentional blink. These results are discussed in light of a neural framework for conscious processing.

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1. Introduction

Every waking moment, the brain is bombarded with an endless stream of incoming sensory information. A relatively minuscule amount of this sensory input is consciously perceived (see Box 1). In order to empirically assess the introspective phenomena of conscious perception, experiments usually obtain a measurement of verbal report (also termed *experiential report*) where the

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subject uses language or some other form of intentionally driven behavior to describe his or her mental state (Baars, 1997; Dehaene & Naccache, 2001).

Box 1. Definitions of frequently used terms. Each term may have multiple meanings, but the definition found below signifies the meaning utilized throughout the paper.

Conscious Perception—awareness of a sensory stimulus

Attention—those operations which voluntarily *select* conscious events amongst a stream of competing sensory information

Working Memory—those operations which *maintain* conscious events in a form which is available for report

Previous neuroimaging studies have investigated the neural mechanisms underlying conscious perception by using a variety of experimental paradigms including binocular rivalry (Lumer, Friston, & Rees, 1998; Lumer & Rees, 1999), masking (Bar et al., 2001; Dehaene et al., 2001; Whalen et al., 1998), change blindness (Beck, Rees, Frith, & Lavie, 2001), inattention blindness (Rees, Russell, Frith, & Driver, 1999), subliminal stimulation (Kjaer, Nowak, Kjaer, Lou, & Lou, 2001), sensory learning (McIntosh, Rajah, & Lobaugh, 1999; Stephan et al., 2002), and lesion studies (Driver & Mattingley, 1998; Vuilleumier et al., 2002). The findings of these studies can be summarized as follows: (1) attention and working memory (see Box 1) are essential ingredients of conscious perception and involve activation of a frontoparietal network (Courtney, Petit, Haxby, & Ungerleider, 1998; Driver & Vuilleumier, 2001; Lumer et al., 1998; Lumer & Rees, 1999; Posner & Rothbart, 1998; Rees & Lavie, 2001; Rees et al., 1999; Treisman & Kanwisher, 1998); (2) stimuli which do not reach awareness may still generate activation in their corresponding sensory cortices (Bar et al., 2001; Beck et al., 2001; Dehaene et al., 2001; Lumer et al., 1998; Lumer & Rees, 1999; Rees & Lavie, 2001; Vuilleumier et al., 2002); (3) awareness is a product of large-scale interactions between many regions of the brain (Bar et al., 2001; Dehaene & Naccache, 2001; Kjaer et al., 2001; McIntosh et al., 1999; Rees & Lavie, 2001); and (4) certain regions within the ventral visual stream are specialized for processing a specific type of information (e.g., color) and any damage to these regions results in a selective loss of awareness (e.g., damage to color-selective areas in the ventral occipitotemporal cortex leads to an inability to perceive colors) (Rees, Kreiman, & Koch, 2002).

The above findings have all made an important contribution toward science's understanding of conscious perception. However, the field is still very young and there is an on-going need for additional research using different experimental paradigms. One such paradigm, the attentional blink, can be used to probe how sensory information gains access to awareness (Dehaene, Sergent, & Changeux, 2003; Luck, Vogel, & Shapiro, 1996). To date, there has only been one other functional neuroimaging study using the attentional blink paradigm (Marois, Chun, & Gore, 2000). The study focused on finding the neural correlates of increased distractor processing. Their findings implicate a primarily right parietofrontal network associated with increased processing demands. Due to their experimental design, Marois et al. were unable to determine which brain areas are specifically involved in conscious perception (Marois et al., 2000). The present study allows for such an analysis.

2. Methods

In the attentional blink paradigm (Fig. 1), multiple strings of letters and numbers are presented in a rapid serial visual presentation (RSVP). Embedded within this RSVP are two targets. The first target (T1) is either an odd or an even string of numbers (e.g., 1111111 or 2222222). The second target (T2) is either a neutral or an aversive word. T2 appears either three items after T1 (Lag 3) or seven items after T1 (Lag 7). Subjects are instructed to focus their eyes on the RSVP and then answer two forced-choice questions. The first question asks whether T1 was odd or even. The second question asks whether or not a particular word was seen. Previous experiments (Luck et al., 1996; Marois et al., 2000; Vogel, Luck, & Shapiro, 1998) have shown that when T1 is correctly identified, there is a period of time (ranging from 200 to 500 ms after the presentation of T1) when it becomes extremely difficult to detect subsequent items in the RSVP. If T2 is presented within this time frame (i.e., at Lag 3), there is a high probability that it will not be detected. This deficit in correctly reporting T2 is known as the “attentional blink” (AB). However, when T2 is presented outside of the 200–500 ms AB time-window (i.e., it is presented at Lag 7), it is easily detected.

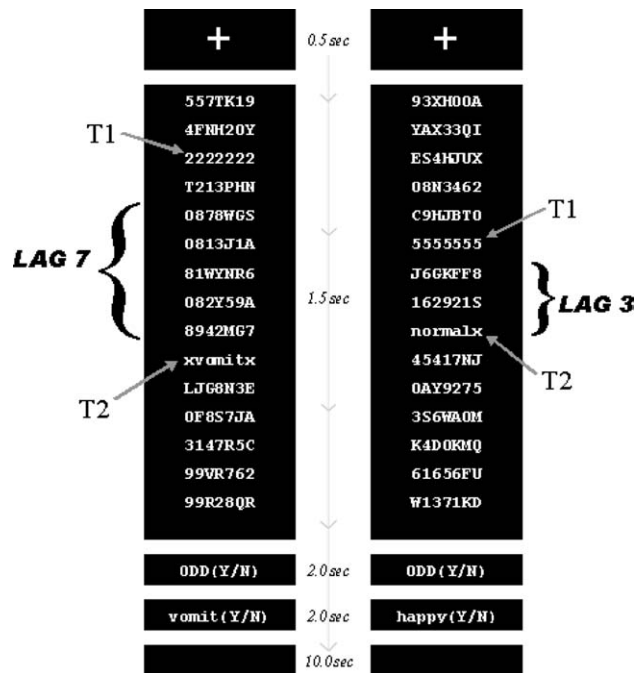


Fig. 1. Two exemplary trials within the attentional blink paradigm used in this study (constructed based on a similar version previously reported (Luck et al., 1996)). Each trial is 16 s long and is composed of a cross fixation, an RSVP, two questions, and a rest period. There were a total of 32 trials in the entire task. Each item in the RSVP is presented for 83 ms, with an interstimulus interval of 17 ms. T1 is placed in either the third or the sixth position of the RSVP and is odd 3/4 of the trials and even 1/4 of trials. T2 is placed in half of the trials at Lag 3 and in half of the trials at Lag 7. The location of T1 and T2 in the RSVP is randomized. The word probed in the second question matches T2 in half of the trials and is some other word (randomly chosen) in the other half of the trials. All 32 trials (with the above combinations) were randomized.

2.1. Subjects

Twenty healthy college students were tested using the AB paradigm in an event-related design during functional magnetic resonance imaging (fMRI). Prior to their participation, all subjects gave their informed, written consent to participate in the study which was approved by the UCSD Human Research Protection Program.

As described in the Section 3.1, four subjects were excluded based on extremely poor behavioral results. The remaining 16 subjects were divided into two groups: the “Blinkers” and the “Non-Blinkers” (see Section 3.1). Each group is composed of 7 females and 1 male subject, all of whom are right handed and native English speakers. Both the Blinkers and the Non-Blinkers have a mean age of 18.6 years (age range, 18–20 years) and an average education of 12.7 years (education range, 12–14 years).

2.2. fMRI design

One functional imaging run sensitive to blood oxygenation level-dependent (BOLD) contrast was collected for each subject using a 1.5-Tesla Siemens (Erlangen, Germany) scanner (T2*-weighted echo-planar imaging, TR = 2000 ms, TE = 40 ms, 64 × 64 matrix, 20 4-mm axial slices, 256 scans). fMRI volume acquisitions were time-locked to the onset of each trial. During the same experimental session, a T1-weighted image (MPRAGE, TR = 11.4 ms, TE = 4.4 ms, flip angle = 10°, FOV = 256 × 256, 1 mm³ voxels) was obtained for anatomical reference.

The attentional blink paradigm (Fig. 1) was presented to the subjects using an LCD projector. The images were back-projected onto a screen near the subject's feet, which could be seen via a mirror attached to the head coil (visual angle ~4°). Subjects requiring corrective lenses were provided with a pair of plastic-framed lenses that approximated their degree of correction. Motor responses were made by the right hand using a button box.

2.3. fMRI analysis

All data was preprocessed, normalized to Talairach coordinates (Talairach & Tournoux, 1988) and analyzed with the software AFNI (Cox, 1996). For preprocessing, voxel time series data were interpolated to correct for non-simultaneous slice acquisition within each volume and corrected for three-dimensional motion. Motion corrected voxel time series data were visually inspected to remove large movement artifacts. Preprocessed time series data for each subject were analyzed using an orthogonal multiple regression model consisting of six regressors. An orthogonal regressor of interest (representing the RSVP during Lag 3 trials) was convolved with a gamma variate function modeling a prototypical hemodynamic response prior to inclusion in the regression model. In addition three regressors were used to model residual motion (in the roll, pitch, and yaw direction) and a baseline regressor as well as a linear trend for the experimental session were used to eliminate slow signal drifts.

The echoplanar images were realigned to the 128th acquired scan and time-corrected for slice acquisition order. To exclude the voxels showing an artifact related signal drop, a combined threshold/cluster-growing algorithm was applied to the mean of the functional images to compute a whole-brain mask. This screened out non-brain voxels and voxels falling within the artifact

region. The AFNI program 3dDeconvolve (Cox, 1996) was used to calculate the estimated voxel-wise impulse response function. A Gaussian filter with FWHM 4 mm was applied to voxel-wise percent signal change data to account for individual variations of anatomical landmarks. The data of each subject were normalized to Talairach coordinates (Talairach & Tournoux, 1988). A threshold adjustment method based on Monte-Carlo simulations was used to guard against identifying false positive areas of activation (Forman et al., 1995). Based on these simulations, it was determined that a voxel-wise a priori probability of 0.05 would result in a corrected cluster-wise activation probability of 0.05 if a minimum volume of 500 μl and a connectivity radius of 4.0 mm was considered.

The voxel-wise percent signal change data was entered into a mixed model ANOVA with group (Blinkers versus Non-Blinkers) as a fixed factor and subjects as a random factor. The resulting functional regions of interest were compared to the brain's estimated hemodynamic response function to an event occurring within the RSVP. First, the BOLD signal within each voxel of activation was extracted for each subject across the entire functional run. Second, each group's average BOLD signal was then calculated with respect to the time course of each trial. The results were then mapped onto a graph (Fig. 3C).

3. Results

3.1. Behavioral results

The behavioral results are calculated based on each subject's response to the two questions asked after each trial. A trial only counts when T1 is correctly identified as either odd or even. Four subjects were excluded based on extremely poor behavioral results. During the Lag 7 period (where it has previously been shown that T2 is correctly reported the majority of the trials (Luck et al., 1996; Marois et al., 2000; Vogel et al., 1998)) the excluded subjects correctly identified T2 an

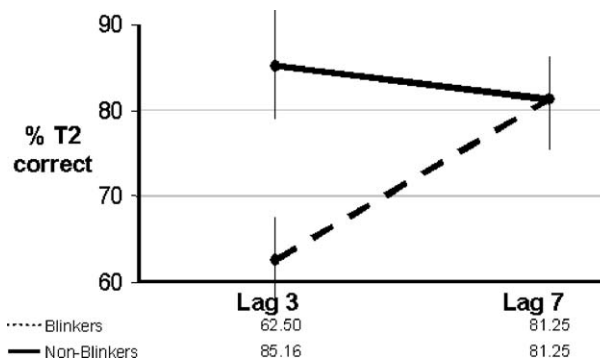


Fig. 2. Behavioral results of the Blinkers and the Non-Blinkers. Notice the AB (deficit in reporting T2 at Lag 3) for the Blinkers, but not the Non-Blinkers. This is a statistically significant difference of 22.7% (group by lag interaction with T1 performance as a covariate: $F(1, 13) = 79.0, p < 0.01$). Both groups performed equally at Lag 7. The thin black lines represent the standard error of the mean. Chance level is 50%.

average of 42% of the time. Inclusion of these subjects would lead to additional noise in the fMRI data, deeming it appropriate and necessary to exclude these subjects.

The behavioral data (Fig. 2) of the remaining 16 subjects revealed an unexpected dichotomy. It was found that this pool of subjects could be further subdivided into two groups of 8 subjects each. The first group of subjects (which will be referred to as the “Blinkers”) correctly identified T2 at Lag 3 less frequently than at Lag 7, thus revealing an expected AB. The second group of subjects (which will be referred to as the “Non-Blinkers”) correctly identified T2 at Lag 3 as often or more often than at Lag 7. In other words, the Non-Blinkers (but not the Blinkers) were able to consciously report T2 during the critical period for the AB. However, both groups performed equally on Lag 7 trials. Furthermore, the Blinkers correctly identified T1 an average of 90.2% ($SEM = \pm 2.6\%$) of the trials and the Non-Blinkers correctly identified T1 an average of 92.6% ($SEM = \pm 4.2\%$) of the trials. The group analysis showed that this difference was not significant

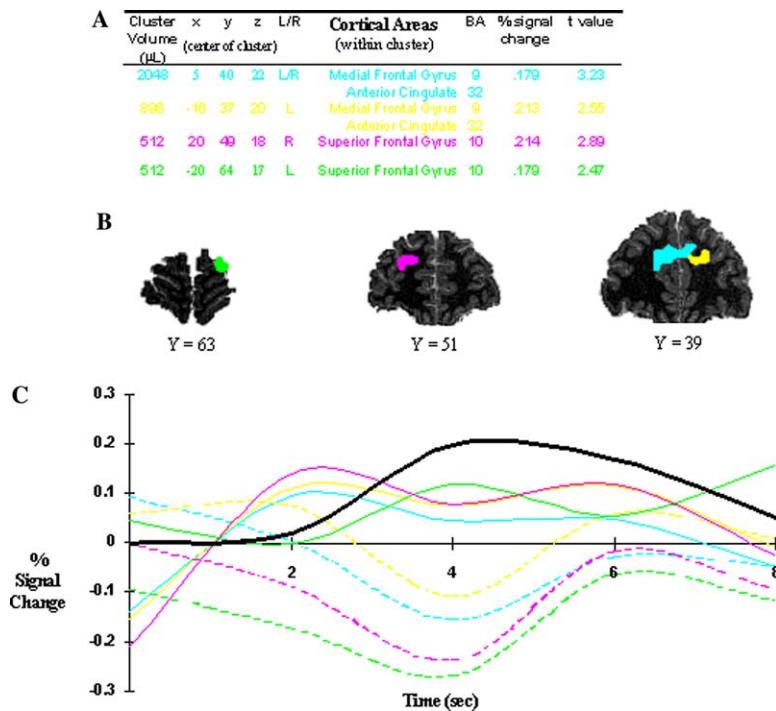


Fig. 3. Clusters of brain activation associated with the Non-Blinkers subsequent conscious perception of T2. (A) Chart of the four functional regions of interest (fROIs) that significantly activated more for the Non-Blinkers than the Blinkers during Lag 3 trials of the RSVP. Cortical areas are based on Talairach Daemon software (Lancaster et al., 2000). (B) Brain areas listed in the chart are color-coded and superimposed on coronal sections of a template brain. (C) Graph of each group's time series data. The plot starts at the onset of the trial (time = 0 s) and ends 8 s into the trial. The *solid lines* are the Non-Blinkers and the *dashed-lines* are the Blinkers (each line is color-coded to match the brain areas in (A and B)). The *solid black line* represents the estimated prototypical hemodynamic response function in the brain corresponding to an event happening during the RSVP (time = 0.5–2.0 s). Notice that the Non-Blinkers had 3 fROIs (pink, yellow, and blue) peak in activation over 2 s prior to the estimated peak in BOLD signal. The Blinkers all deactivate in an inverse relationship with the estimated hemodynamic response. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this paper.)

($t(14) = 0.57, NS$). What patterns of brain activation can account for the Non-Blinkers' success in detecting T2 during Lag 3 trials?

3.2. *fMRI results*

The fMRI results revealed four different areas in the brain that activated significantly more for the Non-Blinkers than the Blinkers during Lag 3 trials of the RSVP (Figs. 3A and B). These four functional regions of interest (fROIs) were observed bilaterally within the medial prefrontal cortex (BA 9), the anterior cingulate (BA 32), and the frontopolar region of the superior frontal gyrus (BA 10).

Due to the poor temporal resolution of fMRI, it is impossible to separate the brain activation elicited by each item in the RSVP (Marois et al., 2000). However, if the entire RSVP is analyzed as an event, then the hemodynamic response within the brain provides a relatively accurate estimate of how the BOLD signal changes over time in response to the RSVP (Burock, Buckner, Woldorff, Rosen, & Dale, 1998; Rosen, Buckner, & Dale, 1998). Treisman and Kanwisher have recently reviewed the literature and have concluded that it takes 100–200 ms (after stimulus presentation) for object recognition to occur and approximately another 100 ms to bring this information into awareness (Treisman & Kanwisher, 1998). If these temporal dynamics are reasonably accurate, then the transferring of T2 into awareness occurs sometime during the RSVP. Therefore, an estimated hemodynamic response function to an event (which occurs sometime during the RSVP) was created and compared with the actual BOLD response time-series data in each cluster of brain activation. The resulting graph (Fig. 3C) provides a clear picture of how each fROI activated over the course of a trial. Relative to the Blinkers, the Non-Blinkers showed an amplified BOLD signal (in each of the four fROIs) in response to the RSVP. Specifically, the anterior cingulate, medial prefrontal cortex, and right superior frontal gyrus reached a peak in activation nearly 2 s prior to the estimated peak in hemodynamic response. The left superior frontal gyrus closely modeled the hemodynamic response function. In contrast, the Blinkers all deactivated in an inverse relationship with the estimated hemodynamic response. Therefore, the Non-Blinkers efficiently activated the anterior cingulate, medial prefrontal cortex, and frontopolar cortex in response to the RSVP during Lag 3 trials, whereas the Blinkers did not. Additionally, during these set of trials the Non-Blinkers consciously perceived T2, whereas the Blinkers were deficient in their awareness of T2.

4. Discussion

These results are consistent with the hypothesis that the behavioral difference in awareness for T2 may be a result of the Non-Blinkers' ability to efficiently activate a network of brain tissue within a circumscribed area of the frontal cortex. The anterior cingulate, medial prefrontal cortex, and frontopolar cortex are anatomically linked by direct, reciprocal connections (Allman, Ha-keem, & Watson, 2002; Bush, Luu, & Posner, 2000). Many other studies have also shown an increase of frontal activation during the transition to a conscious state (the frontal activation tends to be localized to more dorsolateral regions in comparison to the frontal activity found in this study) (Beck et al., 2001; Dehaene et al., 2001; Kjaer et al., 2001; Lumer et al., 1998; Lumer &

Rees, 1999; McIntosh et al., 1999; Rees & Lavie, 2001; Stephan et al., 2002). Furthermore, our contrastive analysis compared two groups of subjects who saw the same exact sensory information, correctly identified the first target, and made the same forced-choice response following each RSVP. This increases the chances that the frontal activation found in Non-Blinkers during Lag 3 trials is related more to the executive interpretation of the conscious signal for the second target rather than some element of response preparation (Lumer & Rees, 1999).

The results of this study coincide with a large body of research studying attention and working memory. The anterior cingulate has been labeled as the central executive for attentional processing, regulating both cognition and emotion (Allman et al., 2002; Bush et al., 2000; Cohen, Botvinick, & Carter, 2000; Devinsky, Morrell, & Vogt, 1995; Posner & Rothbart, 1998). Additionally, the anterior cingulate is hypothesized to be an essential neural substrate underlying consciousness (Damasio, 1999; Dehaene & Naccache, 2001) and has been found to activate to a visually presented word prior to any semantic processing (Abdullaev & Posner, 1998; Posner & Rothbart, 1998). Most studies of awareness have not found activation in the frontopolar cortex. However, there has been one study which implicates the right frontopolar cortex (BA 10) in the conscious perception of a briefly presented word (Kjaer et al., 2001). Some researchers argue that the attentional blink is not a failure of working memory, but rather a failure to properly update working memory with a reportable representation of T2 (Vogel et al., 1998). A network consisting of lateral prefrontal areas and regions within the parietal cortex is responsible for keeping items “online” for a short amount of time (Chafee & Goldman-Rakic, 1998; Courtney et al., 1998), whereas the frontopolar region of the superior frontal gyrus (BA 10) has been argued to be a critical neural substrate for updating verbal working memory (Braver & Bongiolatti, 2002; Collette & Van der, 2002; Van der et al., 1999). Since activity in this region was found in our study, we hypothesize that the attentional blink was abolished for the Non-Blinkers because a reportable representation of T2 had been properly updated into working memory.

Interestingly, when the analysis is performed the opposite way (i.e., brain areas more active for the Blinkers during Lag 3 trials of the RSVP) a completely different pattern of activation is found. In this case, the Blinkers exhibit widespread activation in relatively posterior areas of the brain including visual areas (bilateral thalamus along with both dorsal and ventral visual streams) (Courtney & Ungerleider, 1997), word processing areas (left lingual gyrus, left angular gyrus, left anterior insula, and bilateral superior temporal gyrus) (Abdullaev & Posner, 1998; Price, 2000), and somatosensory areas (right insula and right somatosensory cortex) (Damasio, 1999). However, no clusters of activation were found in the prefrontal cortex or anterior cingulate. It is difficult to speculate why this particular pattern of widespread posterior activation was found in the Blinkers but not the Non-Blinkers during Lag 3 trials. Perhaps the lack of frontal activation in the Blinkers relates to their inability to bind together the individual visual features of T2 (Kanwisher, 2001)? Previous studies have generally reported a reduction in activity (especially within the ventral visual stream) elicited by a visual stimulus which is not consciously perceived (Bar et al., 2001; Beck et al., 2001; Dehaene et al., 2001; Lumer et al., 1998; Lumer & Rees, 1999). However, it is important to note that the present study did not employ a pure unconscious condition since the Blinkers were still able to detect the first target (the odd or even string of numbers). Nevertheless, these results do support a study measuring event-related potentials during a similar attentional blink paradigm (Luck et al., 1996). Their results show that T2 can evoke widespread sensory and semantic related processes even when it is not consciously

perceived. This concurs with our finding of the Blinkers activation in visual and word processing brain regions.

Taken together, these results are best viewed in light of a theory developed by Baars and expanded upon by Dehaene (Baars, 1983; Baars, 2002; Dehaene & Naccache, 2001; Dehaene et al., 2003). This theory of consciousness, known as the global neuronal workspace, argues that many different cortical and sub-cortical networks are active during unconscious processing and it takes an executive component (mainly the anterior cingulate and other prefrontal regions) to mobilize these networks into a state of coherent activity resulting in a conscious state. The conscious state is not produced by a single region of the brain, but is rather a by-product of information from a multitude of regions being communicated and amplified throughout the brain. The anterior cingulate, along with other prefrontal regions, is thought to play an important role in the selection and amplification of what information is broadcasted to the rest of the brain (Dehaene & Naccache, 2001; Dehaene et al., 2003).

4.1. Anterior cingulate

The region of the anterior cingulate found to activate in this study is anatomically located at the junction of the cognitive and affective subdivisions, thereby providing easy-access to strong interconnections with the lateral prefrontal cortex (BA 46/9), parietal cortex (BA 7), anterior insula, orbitofrontal cortex, hippocampus, and many other somatosensory, motor, autonomic and endocrine systems (Bush et al., 2000). Furthermore, the anterior cingulate cortex receives a massive amount of visual input projected via the thalamus and other higher-order sensory cortices (Bush et al., 2000; Damasio, 1999; Devinsky et al., 1995). Since most of these connections are reciprocal, the anterior cingulate is able to integrate large quantities of information while modulating activity in a vast amount of other brain areas via feedback signals (Cohen et al., 2000; Damasio, 1999). Previous studies have implicated the anterior cingulate in a wide variety of processes ranging from conflict monitoring and error detection to emotional regulation (Bush et al., 2000). This study adds to the list of processes by finding anterior cingulate activation related to conscious perception of a sensory stimulus.

4.2. Medial prefrontal cortex

The region of the medial prefrontal cortex found to activate in this study nicely overlaps with activation found in a variety of neuroimaging studies studying the elusive concept of mentalizing/theory of mind (for a review see Frith & Frith, 2003). This region seems to be engaged whenever we attend to our own mental states as well as to the mental states of others (Frith & Frith, 2003). It is intriguing to think that conscious perception may be intimately linked with the uniquely human ability to mentalize.

4.3. Frontopolar cortex

The functional role of the frontopolar cortex is not clearly understood and warrants further study. Its specific role in the attentional blink paradigm is further emphasized by a patient with a bilateral frontopolar lesion who has an abnormal attentional blink length and magnitude (Rizzo,

Akutsu, & Dawson, 2001). Here, we show bilateral superior frontopolar (BA 10) activation which is involved in successfully detecting two targets in a rapid stream of distractors. This finding sits well with a recent theory proposed by Braver and Bongiolatti (Braver & Bongiolatti, 2002). They hypothesize that the frontopolar cortex may be engaged whenever the results of subgoal processing need to be integrated with the information stored in working memory. Subjects in our task had to maintain the subgoals of detecting two different targets (an odd or even string of numbers and a word) while viewing a rapid stream of distractors. Once the word is identified, we argue that it is updated into working memory by the frontopolar cortex. In addition, a recent study (Dreher, Koehlin, Ali, & Grafman, 2002) reports left frontopolar activation that was correlated with the subject's level of preparation, suggesting that the Non-Blinkers may have been better prepared to perform the task.

4.4. Parietal cortex

The right parietal cortex has been implicated as an essential neural substrate underlying spatial attention processes (Driver & Vuilleumier, 2001; Marois et al., 2000). Damage to this area may result in the subsequent loss of awareness for stimuli located in the contralesional side of space; a condition known as neglect (Driver & Vuilleumier, 2001). Marois et al. found significant activation within the right intraparietal sulcus while subjects performed a variation of the attentional blink paradigm with different degrees of perceptual interference (Marois et al., 2000). The parietal cortex is undoubtedly an essential component of awareness and attentional blink processing, but was not found to activate in the current study.

4.5. Limitations and future directions

This study is the first to use the attentional blink paradigm with functional neuroimaging to probe how sensory information gains access to awareness. The results must be interpreted with caution until they are replicated by future studies using similar methodology. The only previous study to use the attentional blink paradigm with fMRI (Marois et al., 2000) did not include the second target in the RSVP, thereby making it impossible to specifically analyze the neural mechanisms underlying conscious perception for T2. Our serendipitous finding of Non-Blinkers (who were able to accurately detect the second target) allowed for a unique contrastive analysis of Lag 3 trials. To our knowledge, we do not know of any other papers reporting a group of subjects who were able to override the attentional blink. Unfortunately, we did not obtain any neuropsychological measurements which would relate to attention, memory, or frontal lobe functioning. Therefore, we cannot draw any conclusions as to why the Non-Blinkers performed so well.

Recent work by Dehaene et al. suggests that the attentional blink may be an all or none phenomena (i.e., on a single trial, a subject can either report seeing the second target or claims not to see the target at all) (Dehaene et al., 2003). This leaves open the future possibility of using single-event fMRI, which would allow for a more precise analysis of neural activity underlying T2 detection.

The limited number of trials in our paradigm precluded us from doing any analysis incorporating word valence (neutral versus aversive). Since this study's goal was to elucidate neural activity specifically involved in conscious perception, we do not feel that the use of affective words discredit the current findings. A previous study by Anderson and colleagues has already estab-

lished the importance of the amygdala in detecting aversive words hidden within the RSVP (Anderson & Phelps, 2001). It will be important for future studies to further explore the neural processes underlying conscious perception of aversive words (this work is currently underway in our laboratory).

5. Conclusion

Activation of the anterior cingulate, medial prefrontal cortex, and frontopolar cortex was found to be involved in the conscious perception of the second target in an attentional blink paradigm. These results support a global workspace theory which posits that consciousness is a product of dynamic large-scale interactions between many regions of the brain. Thus, the Non-Blinkers utilized the top-down attentional amplification of executive prefrontal regions in order to transform a fleeting sensory perception into the “knowing-state” of awareness.

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References

- Abdullaev, Y. G., & Posner, M. I. (1998). Event-related brain potential imaging of semantic encoding during processing single words. *Neuroimage*, *7*, 1–13.
- Allman, J., Hakeem, A., & Watson, K. (2002). Two phylogenetic specializations in the human brain. *Neuroscientist*, *8*, 335–346.
- Anderson, A. K., & Phelps, E. A. (2001). Lesions of the human amygdala impair enhanced perception of emotionally salient events. *Nature*, *411*, 305–309.
- Baars, B. J. (1983). Conscious contents provide the nervous system with coherent, global information. In R. Davidson, G. Schwartz, & D. Shapiro (Eds.), *Consciousness and self-regulation* (Vol. 2, pp. 45–76). New York: Plenum.
- Baars, B. J. (1997). Some essential differences between consciousness and attention, perception, and working memory. *Consciousness and Cognition*, *6*, 363–371.
- Baars, B. J. (2002). The conscious access hypothesis: Origins and recent evidence. *Trends in Cognitive Sciences*, *6*, 47–52.
- Bar, M., Tootell, R. B., Schacter, D. L., Greve, D. N., Fischl, B., Mendola, J. D., Rosen, B. R., & Dale, A. M. (2001). Cortical mechanisms specific to explicit visual object recognition. *Neuron*, *29*, 529–535.
- Beck, D. M., Rees, G., Frith, C. D., & Lavie, N. (2001). Neural correlates of change detection and change blindness. *Nature Neuroscience*, *4*, 645–650.
- Braver, T. S., & Bongiolatti, S. R. (2002). The role of frontopolar cortex in subgoal processing during working memory. *Neuroimage*, *15*, 523–536.
- Burock, M. A., Buckner, R. L., Woldorff, M. G., Rosen, B. R., & Dale, A. M. (1998). Randomized event-related experimental designs allow for extremely rapid presentation rates using functional MRI. *Neuroreport*, *9*, 3735–3739.
- Bush, G., Luu, P., & Posner, M. I. (2000). Cognitive and emotional influences in anterior cingulate cortex. *Trends in Cognitive Sciences*, *4*, 215–222.

- Chafee, M. V., & Goldman-Rakic, P. S. (1998). Matching patterns of activity in primate prefrontal area 8a and parietal area 7ip neurons during a spatial working memory task. *Journal of Neurophysiology*, *79*, 2919–2940.
- Cohen, J. D., Botvinick, M., & Carter, C. S. (2000). Anterior cingulate and prefrontal cortex: Who's in control? *Nature Neuroscience*, *3*, 421–423.
- Collette, F., & Van der, L. M. (2002). Brain imaging of the central executive component of working memory. *Neuroscience and Biobehavioral Reviews*, *26*, 105–125.
- Courtney, S. M., Petit, L., Haxby, J. V., & Ungerleider, L. G. (1998). The role of prefrontal cortex in working memory: Examining the contents of consciousness. *Philosophical Transactions of the Royal Society of London B Biological Sciences*, *353*, 1819–1828.
- Courtney, S. M., & Ungerleider, L. G. (1997). What fMRI has taught us about human vision. *Current Opinion in Neurobiology*, *7*, 554–561.
- Cox, R. W. (1996). AFNI: Software for analysis and visualization of functional magnetic resonance neuroimages. *Computers and Biomedical Research*, *29*, 162–173.
- Damasio, A. R. (1999). *The feeling of what happens*. New York: Harcourt.
- Dehaene, S., Naccache, L., Cohen, L., Bihan, D. L., Mangin, J. F., Poline, J. B., & Riviere, D. (2001). Towards a cognitive neuroscience of consciousness: Basic evidence and a workspace framework. *Cognition*, *79*, 1–37.
- Dehaene, S., Naccache, L., Cohen, L., Bihan, D. L., Mangin, J. F., Poline, J. B., et al. (2001). Cerebral mechanisms of word masking and unconscious repetition priming. *Nature Neuroscience*, *4*, 752–758.
- Dehaene, S., Sergent, C., & Changeux, J. P. (2003). A neuronal network model linking subjective reports and objective physiological data during conscious perception. *Proceedings of the National Academy of Sciences of the United States of America*, *100*, 8520–8525.
- Devinsky, O., Morrell, M. J., & Vogt, B. A. (1995). Contributions of anterior cingulate cortex to behaviour. *Brain*, *118*(Pt 1), 279–306.
- Dreher, J. C., Koechlin, E., Ali, S. O., & Grafman, J. (2002). The roles of timing and task order during task switching. *Neuroimage*, *17*, 95–109.
- Driver, J., & Mattingley, J. B. (1998). Parietal neglect and visual awareness. *Nature Neuroscience*, *1*, 17–22.
- Driver, J., & Vuilleumier, P. (2001). Perceptual awareness and its loss in unilateral neglect and extinction. *Cognition*, *79*, 39–88.
- Forman, S. D., Cohen, J. D., Fitzgerald, M., Eddy, W. F., Mintun, M. A., & Noll, D. C. (1995). Improved assessment of significant activation in functional magnetic resonance imaging (fMRI): Use of a cluster-size threshold. *Magnetic Resonance in Medicine*, *33*, 636–647.
- Frith, U., & Frith, C. D. (2003). Development and neurophysiology of mentalizing. *Philosophical Transactions of the Royal Society of London B Biological Sciences*, *358*, 459–473.
- Kanwisher, N. (2001). Neural events and perceptual awareness. *Cognition*, *79*, 89–113.
- Kjaer, T. W., Nowak, M., Kjaer, K. W., Lou, A. R., & Lou, H. C. (2001). Precuneus-prefrontal activity during awareness of visual verbal stimuli. *Consciousness and Cognition*, *10*, 356–365.
- Lancaster, J. L., Woldorff, M. G., Parsons, L. M., Liotti, M., Freitas, C. S., Rainey, L., Kochunov, P. V., Nickerson, D., Mikiten, S. A., & Fox, P. T. (2000). Automated Talairach atlas labels for functional brain mapping. *Human Brain Mapping*, *10*, 120–131.
- Luck, S. J., Vogel, E. K., & Shapiro, K. L. (1996). Word meanings can be accessed but not reported during the attentional blink. *Nature*, *383*, 616–618.
- Lumer, E. D., Friston, K. J., & Rees, G. (1998). Neural correlates of perceptual rivalry in the human brain. *Science*, *280*, 1930–1934.
- Lumer, E. D., & Rees, G. (1999). Covariation of activity in visual and prefrontal cortex associated with subjective visual perception. *Proceedings of the National Academy of Sciences of the United States of America*, *96*, 1669–1673.
- Marois, R., Chun, M. M., & Gore, J. C. (2000). Neural correlates of the attentional blink. *Neuron*, *28*, 299–308.
- McIntosh, A. R., Rajah, M. N., & Lobaugh, N. J. (1999). Interactions of prefrontal cortex in relation to awareness in sensory learning. *Science*, *284*, 1531–1533.
- Posner, M. I., & Rothbart, M. K. (1998). Attention, self-regulation and consciousness. *Philosophical Transactions of the Royal Society of London B Biological Sciences*, *353*, 1915–1927.

- Price, C. J. (2000). The anatomy of language: Contributions from functional neuroimaging. *Journal of Anatomy*, 197(Pt 3), 335–359.
- Rees, G., Kreiman, G., & Koch, C. (2002). Neural correlates of consciousness in humans. *Nature Reviews Neuroscience*, 3, 261–270.
- Rees, G., & Lavie, N. (2001). What can functional imaging reveal about the role of attention in visual awareness? *Neuropsychologia*, 39, 1343–1353.
- Rees, G., Russell, C., Frith, C. D., & Driver, J. (1999). Inattention blindness versus inattention amnesia for fixated but ignored words. *Science*, 286, 2504–2507.
- Rizzo, M., Akutsu, H., & Dawson, J. (2001). Increased attentional blink after focal cerebral lesions. *Neurology*, 57, 795–800.
- Rosen, B. R., Buckner, R. L., & Dale, A. M. (1998). Event-related functional MRI: Past, present, and future. *Proceedings of the National Academy of Sciences of the United States of America*, 95, 773–780.
- Stephan, K. M., Thaut, M. H., Wunderlich, G., Schicks, W., Tian, B., Tellmann, L., Schmitz, T., Herzog, H., McIntosh, G. C., Seitz, R. J., & Homberg, V. (2002). Conscious and subconscious sensorimotor synchronization—prefrontal cortex and the influence of awareness. *Neuroimage*, 15, 345–352.
- Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain*. Stuttgart, New York: Thieme Medical Publishers.
- Treisman, A. M., & Kanwisher, N. G. (1998). Perceiving visually presented objects: Recognition, awareness, and modularity. *Current Opinion in Neurobiology*, 8, 218–226.
- Van der, L. M., Collette, F., Salmon, E., Delfiore, G., Degueldre, C., & Luxen, A. (1999). The neural correlates of updating information in verbal working memory. *Memory*, 7, 549–560.
- Vogel, E. K., Luck, S. J., & Shapiro, K. L. (1998). Electrophysiological evidence for a postperceptual locus of suppression during the attentional blink. *Journal of Experimental Psychology Human Perception and Performance*, 24, 1656–1674.
- Vuilleumier, P., Armony, J., Clarke, K., Husain, M., Driver, J., & Dolan, R. (2002). Neural response to emotional faces with and without awareness: Event-related fMRI in a parietal patient with visual extinction and spatial neglect. *Neuropsychologia*, 40, 2156.
- Whalen, P. J., Rauch, S. L., Etcoff, N. L., McInerney, S. C., Lee, M. B., & Jenike, M. A. (1998). Masked presentations of emotional facial expressions modulate amygdala activity without explicit knowledge. *Journal of Neuroscience*, 18, 411–418.