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Backward masked fearful faces enhance contralateral occipital cortical activity for visual targets within the spotlight of attention

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Spatial attention has been argued to be adaptive by enhancing the processing of visual stimuli within the 'spotlight of attention'. We previously reported that crude threat cues (backward masked fearful faces) facilitate spatial attention through a network of brain regions consisting of the amygdala, anterior cingulate and contralateral visual cortex. However, results from previous functional magnetic resonance imaging (fMRI) dot-probe studies have been inconclusive regarding a fearful face-elicited contralateral modulation of visual targets. Here, we tested the hypothesis that the capture of spatial attention by crude threat cues would facilitate processing of subsequently presented visual stimuli within the masked fearful face-elicited 'spotlight of attention' in the contralateral visual cortex. Participants performed a backward masked fearful face dot-probe task while brain activity was measured with fMRI. Masked fearful face left visual field trials enhanced activity for spatially congruent targets in the right superior occipital gyrus, fusiform gyrus and lateral occipital complex, while masked fearful face right visual field trials enhanced activity in the left middle occipital gyrus. These data indicate that crude threat elicited spatial attention enhances the processing of subsequent visual stimuli in contralateral occipital cortex, which may occur by lowering neural activation thresholds in this retinotopic location.

Keywords: Emotion; spatial attention; facial expressions; restricted awareness; affective neuroscience

INTRODUCTION

The direction of cognitive resources to specific retinotopic locations in visual space is an important method by which processing of visual information is prioritized. In general, visual threat signals are salient exogenous cues that automatically capture spatial attention (Ohman *et al.*, 2001) and threatening (fearful and angry) facial expressions in particular can capture spatial attention both when restricted/backward masked (Mogg and Bradley, 1999, 2002; Fox, 2002; Carlson and Reinke, 2008) and unrestricted/unmasked (Pourtois, *et al.*, 2004; Cooper and Langton, 2006). Backward masking consists of a brief stimulus presentation (e.g. an initial face) that is followed in close temporal proximity by a 'masking' stimulus presentation (e.g. a second face). The re-entrant processing of the initial stimulus in sensory cortex is thought to be interrupted and replaced by the masking stimulus (Enns and Di Lollo, 2000). Backward masking therefore restricts the processing of the initial stimulus and has been used to assess the sensitivity in which threatening faces influence observers (Whalen *et al.*, 1998; Mogg and Bradley, 1999). Neuroimaging research suggests that backward masked threatening faces enhance

activity within the amygdala (Morris *et al.*, 1998; Whalen *et al.*, 1998), subcortical visual nuclei (Morris *et al.*, 1999), anterior cingulate cortex (ACC; Liddell *et al.*, 2005; Williams *et al.*, 2006), and superior temporal sulcus (STS; Jiang and He, 2006). Recent evidence suggests the amygdala, ACC, STS and contralateral lingual gyrus comprise a neural network involved in orienting spatial attention to backward masked fearful faces (Carlson *et al.*, 2009) and this attentional response modulates early face processing in visual cortex within 170 ms post face onset (Carlson and Reinke, 2010). Collectively, the current literature indicates that backward masked fearful faces rapidly capture spatial attention through an amygdalo-cortical network.

It remains unclear, however, how this attentional response may influence visual stimuli (e.g. targets) that are subsequently located within the fear-elicited 'spotlight of attention' (Posner, 1980). That is, while behavioral studies (in normal Carlson and Reinke, 2008 and in highly anxious populations Fox, 2002; Mogg and Bradley, 1999, 2002) generally report faster reaction times (RTs) for targets following masked threatening faces, it is unclear what type of modulation of sensory cortex underlies this behavioral effect. An unmasked fearful face dot-probe study found greater BOLD-related activity in right lateral occipital cortex for target stimuli that were spatially congruent with fearful face cues (collapsed across visual field), compared to

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spatially incongruent targets (Pourtois *et al.*, 2006), which lead the authors to suggest that the processing of visual stimuli within the site of attentional capture is enhanced. However, it should be noted that this study did not report a cued visual field specific contralateral modulation of visual cortex nor did they report significant behavioral attention effects. Therefore, it is difficult to form clear conclusions about brain–behavior relationships from this study. In a similar event-related potential (ERP) study congruent compared to incongruent (again collapsed across visual field) targets were found to enhance the occipital P1 target evoked potential (Pourtois *et al.*, 2004). Evidence from unmasked non-emotional ERP studies of exogenous spatial attention have revealed contralateral attention-related modulations in occipital N1 or P1 target evoked potentials (Di Russo *et al.*, 2003; Fu *et al.*, 2005; Natale *et al.*, 2006). As a whole neuroimaging research suggests that the processing of target stimuli in visual cortex is modulated by unmasked attention cues. However, evidence for a contralateral modulation of attention has to date only been observed in non-emotion ERP studies. Thus, it is unclear if crude threat signals such as backward masked fearful faces would modulate contralateral visual cortical processing of subsequently presented targets.

The objective of the current investigation was to assess the extent to which backward masked fearful face-elicited spatial attention enhances contralateral occipital cortical processing of targets located within the ‘spotlight of attention’. To address this issue, participants performed an event-related functional magnetic resonance imaging (fMRI) dot-probe task with backward masked fearful faces (Carlson *et al.*, 2009). It was predicted that due to the engagement of attention, backward masked fearful faces would enhance contralateral visual cortical processing for subsequent visual stimuli within the fear-elicited ‘spotlight of attention’. Specifically, we expected that congruent relative to incongruent trials in the left visual field (LVF) would enhance BOLD activation in areas of the right visual cortex, whereas congruent relative to incongruent trials in the right visual field (RVF) would enhance BOLD activity in the left visual cortex.

METHODS

Parts of this dataset have previously been published (Carlson *et al.*, 2009) and the general procedure has previously been described. Here, we perform additional (unreported) analyses to address the aforementioned objective of the current article.

Subjects

Twelve (seven male and five female) right-handed individuals between the ages of 18 and 35 years participated in the study. Potential participants were screened for prescription and recreational drug usage, neurological and psychological histories, and for metal. Participants gave informed consent, were treated in accordance to the guidelines of the

Institutional Review Board at Southern Illinois University Carbondale, and received monetary compensation for their time.

Stimuli and equipment

Stimuli were presented using the IFIS system on an MRI-compatible LCD screen mounted to the head coil with a field of view of 7.5°. Four (two males and two females) gray-scale facial identities of fearful and neutral expressions were used for the initial faces and a fifth neutral female face was used as the mask face. These faces were from a standardized face database (Gur *et al.*, 2002). Facial stimuli were cropped to eliminate hair and other extraneous features. Participant responses were obtained with an IFIS MRI-compatible response pad. The LCD screen and response pad were controlled via a fiber optic cable by a control room PC equipped with E-Prime 1.1 (Psychology Software Tools, Pittsburg, PA, USA). The beginning of the experiment was triggered by the first radiofrequency pulse of the echo planer imaging (EPI) sequence.

Dot-probe task

As can be seen in Figure 1A, each trial of the dot-probe task (MacLeod and Mathews, 1988) began with a 1000-ms fixation cue, which was immediately followed by two faces simultaneously presented (33 ms) to the left and right of fixation (outer edges of the faces were separated by 15° of visual angle). These initial faces were immediately masked by neutral faces (100 ms) offset by approximately 1° of visual angle on the vertical *Y*-axis to minimize apparent motion (Liddell *et al.*, 2005). To reduce biasing participants’ attention to one side of the screen or the other, horizontal shifts were not used. Masks were followed by a LVF or RVF target dot (750 ms) and a jittered (500–2000 ms) intertrial interval. With the IFIS response pad, subjects used their right index finger for LVF targets and right middle finger for RVF targets.

Trials with one fearful and one neutral initial face (with the fearful face occurring equally in either the LVF or RVF) were considered directed spatial attention. These trials were half congruent (target dot on the same side as the fearful face) and half incongruent. On the other hand, trials with either both fearful (FF) or both neutral (NN) 33 ms faces represented undirected attention. Whereas directed attention trials are thought to contain a shift in spatial attention to the location of the fearful face, undirected trials are independent of an attentional bias to one face over the other. Here, we examine the BOLD-related differences between congruent and incongruent directed attention trials to explore the mechanisms in which masked fearful faces modulate the processing of targets within the ‘spotlight of attention’. For BOLD-related differences between directed and undirected attention conditions, see our previous work (Carlson *et al.*, 2009).

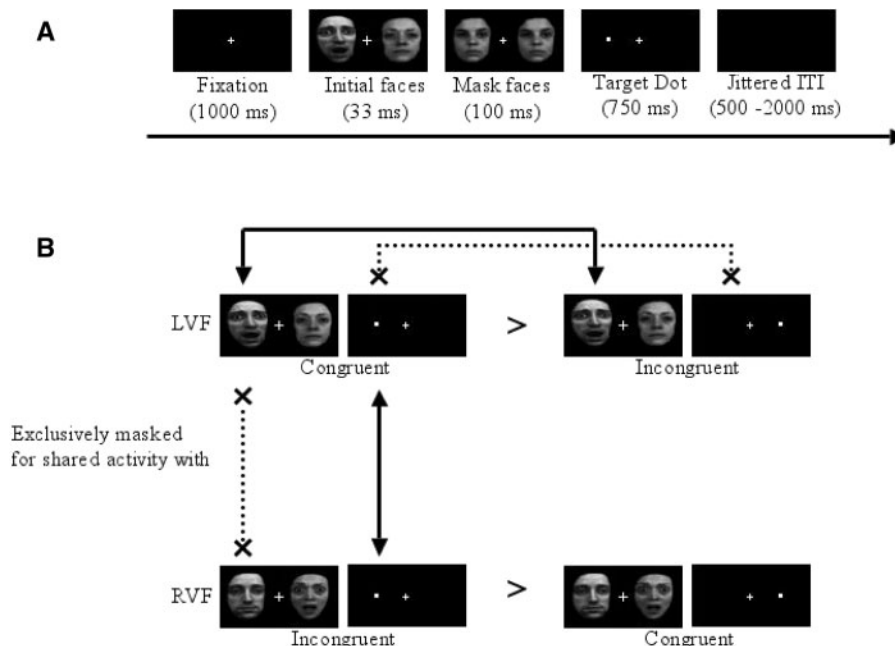


Fig. 1 (A) Each trial (e.g. LVF congruent) began with a fixation cue, which was followed by a set of initial faces (either LVF fear, RVF fear, fearful–fearful, or neutral–neutral). The initial faces were immediately masked with a neutral face and followed by a target dot. (B) Depicted is the LVF congruent > incongruent contrast (top row) that excludes common activity with the RVF incongruent > congruent contrast (bottom row). As can be seen, in LVF congruent trials there is a fearful face and a dot in the LVF, but in LVF incongruent trials there is only a fearful face in the LVF, while the dot is in the RVF. By exclusively masking common activity from the RVF incongruent > congruent contrast, which shares the same dot locations, the remaining activity should only represent masked fearful face spatial attention enhanced target processing. Solid lines indicate similarities between trial types, while dotted lines indicate differences. Facial stimuli are from Gur *et al.*, 2002.

In a previously reported control study implementing the same masking parameters, 14 out of 15 subjects failed to identify the dot-probe trial types above chance (Carlson *et al.*, 2009). Thus, our backward masking procedures appear to be successful at restricting the processing of the initial (masked) faces, but we do not claim that this restricted processing is subliminal or non-conscious *per se*.

Imaging procedures and parameters

The general image acquisition and preprocessing procedures were the same as those reported in Carlson *et al.* (2009). Briefly, a 1.5-T Phillips whole body scanner equipped with a head coil was used to acquire EPI BOLD-sensitive T2* weighted scans using the following parameters: TR = 2500 ms, TE = 50 ms, flip angle = 90°, matrix dimensions = 64 × 64, slices = 26, slice thickness = 5.5 mm, gap = 0. Standard SPM5 (Wellcome Department of Cognitive Neurology, London) preprocessing procedures were performed, including: image realignment corrections for head movements, slice timing corrections, normalization to standard 2 × 2 × 2 mm Montreal Neurological Institute space, and spatial smoothing with a Gaussian full-width at half-maximum 10-mm filter. First-level single subject statistical parameter maps were created for each condition using the general linear model in SPM5. The onset of each trial was time locked to the presentation of the initial (i.e. backward masked) faces. A full factorial second-level model was

created with six levels (LVF: congruent and incongruent, RVF: congruent and incongruent, neutral–neutral, and fearful–fearful). For our new analyses, regions of interest (ROI) masks were created using MARINA (Walter *et al.*, 2003). Left and right occipital cortex ROIs (bilaterally including the superior occipital gyrus (SOG), middle occipital gyrus (MOG), inferior occipital gyrus, cuneus, calcarine fissure, lingual gyrus, and fusiform gyrus (FG) posterior to $y = -38$) were created to assess the facilitation of visual cortex associated with congruent > incongruent activations. ROI analyses were performed using an $\alpha = 0.005$ at 10 continuous voxels.

RESULTS

Behavioral effects

As reported earlier (Carlson *et al.*, 2009), RTs were faster on congruent trials than incongruent trials in the LVF ($P = 0.006$) but did not differ in the RVF ($P = 0.59$).

Neuroimaging effects

Congruent > incongruent activation in LVF and RVF trials should reveal differential lateralized processing in contralateral occipital cortex, which presumably reflects the enhancement of target processing by backward masked fearful face-elicited spatial attention. Based on the behavioral facilitation of LVF, but not RVF trials, greater contralateral enhancement in occipital cortex was expected for LVF trials. To distinguish between spatial attention enhanced

Table 1 Spatial attention related brain activations

Region and analysis	Hemisphere	MNI coordinates			Voxels	<i>t</i> value	<i>P</i> -value
		<i>x</i>	<i>y</i>	<i>z</i>			
Occipital cortex ROI congruent > incongruent							
LVF activations							
FG	R	26	-90	-34	20	3.18	0.001
SOG	R	34	-74	26	43	3.05	0.002
LOC	R	46	-72	-6	12	2.97	0.002
RVF activations							
MOG	L	-44	-84	8	332	4.23	<0.001

target processing and target processing in general, congruent > incongruent activation in each visual field was exclusively masked with incongruent > congruent activation for the opposite visual field (Figure 1B). For example, in LVF congruent trials, there is a fearful face and a dot in the LVF, but in LVF incongruent trials there is only a fearful face in the LVF (the dot is in the RVF). Therefore, one might expect greater contralateral activity during congruent trials simply because there are more visual stimuli (i.e. fearful face and the target dot) in the visual field activating the contralateral visual cortex. Given that RVF incongruent trials contain a LVF target dot, a LVF congruent (dot on left) > LVF incongruent (dot on right) contrast that excludes common RVF incongruent (dot on left) > RVF congruent (dot on right) activity (note that these contrasts contain the same relative dot locations) should solely reflect enhanced target processing due to the target appearing within the spotlight of attention. The LVF congruent > incongruent contrast (exclusively masked by RVF incongruent > congruent activity at $P=0.005$) resulted in activation of the contralateral occipital cortex; specifically, the right SOG, FG and lateral occipital complex (LOC; Table 1). Conversely, the RVF congruent > incongruent contrast (exclusively masked by LVF incongruent > congruent activity at $P=0.005$) revealed contralateral activation of the left MOG (Table 1). Therefore, as presented in Figure 2, the processing of visual targets located within the site of attentional capture was enhanced in contralateral areas of occipital cortex. Similar to the observed behavioral facilitation of LVF (but not RVF) trials, the contralateral enhancement of occipital cortex was more distributed for LVF relative to RVF trials.

To verify that the contralateral congruency effect reported above reflects an interaction, we performed an additional analysis. BOLD data were extracted from the areas of activity for the LVF congruent > incongruent and RVF congruent > incongruent contrasts and included in an analysis of variance to test for a congruency \times visual field \times hemisphere interaction. This analysis revealed a significant interaction [$F(1,11)=30.80$, $P<0.001$], where there was enhanced visual cortical processing on congruent *vs* incongruent trials in the hemisphere contralateral to the cued visual

field. Specifically, follow up Bonferroni corrected *t*-tests revealed greater activation on congruent compared to incongruent trials for cued RVF trials in the LH (mean congruent = 5.32, mean incongruent = -1.95, $P_{\text{corrected}} < 0.01$) and cued LVF trials in the RH (mean congruent = 4.22, mean incongruent = -4.12, $P_{\text{corrected}} < 0.01$). Comparisons between congruent and incongruent trials for each cued visual field in the ipsilateral hemispheres were not significant.

DISCUSSION

The results provide new evidence that the processing of visual stimuli located within the crude threat-elicited 'spotlight of attention' is enhanced at contralateral sites of occipital cortex. In particular, LVF congruent relative to incongruent trials significantly increased activity (i.e. above the activity level for targets occurring in the same location, but not in the spotlight of attention) in the right SOG, FG and LOC, while RVF congruent, relative to incongruent, trials increased activation in the left MOG (Figure 2).

As reported earlier (Carlson *et al.*, 2009), the amygdala, ACC, and contralateral visual cortex appear to comprise a neural network involved in orienting spatial attention to crude threatening faces. This network is consistent with the emotional attention system proposed by Holland and Gallagher (1999) that is thought to influence sensory processing through the cholinergic nucleus basalis diffuse modulatory system. Within this framework, attentional modulation is attributed to the ability of acetylcholine (ACh) to increase the functionally specific response of neurons by lowering their activation thresholds (Sarter *et al.*, 2003). In the current context, ACh release in the retinotopic location previously occupied by a masked fearful face should result in selectively enhancing neural responses within this retinotopically distinct location, which may be associated with the contralateral enhancement of congruent target processing and faster target detection. This model is consistent with previous behavioral findings that visual discrimination (Phelps *et al.*, 2006) and target detection (Carlson and Reinke, 2008) are improved at locations immediately preceded by a fearful face. The facilitation of visual perception may be attributed to the selective amplification of perceptual processing associated with the modulation of spatial attention. Direct amygdala projections to areas in the ventral visual stream (Adolphs, 2004; Vuilleumier *et al.*, 2004) are also expected to play a role in mediating the attentional enhancement of masked fearful face congruent target processing in visual cortex.

Previous studies of unmasked fearful face-elicited spatial attention did not test for (congruent > incongruent) modulations of visual cortex (Armony, and Dolan, 2002) or only reported general (i.e. not cued visual field specific) modulations in visual cortex (Pourtois *et al.*, 2006); however, our results indicate that masked fearful face-elicited spatial attention specifically enhances contralateral occipital cortical activity for congruent compared to incongruent trials. This

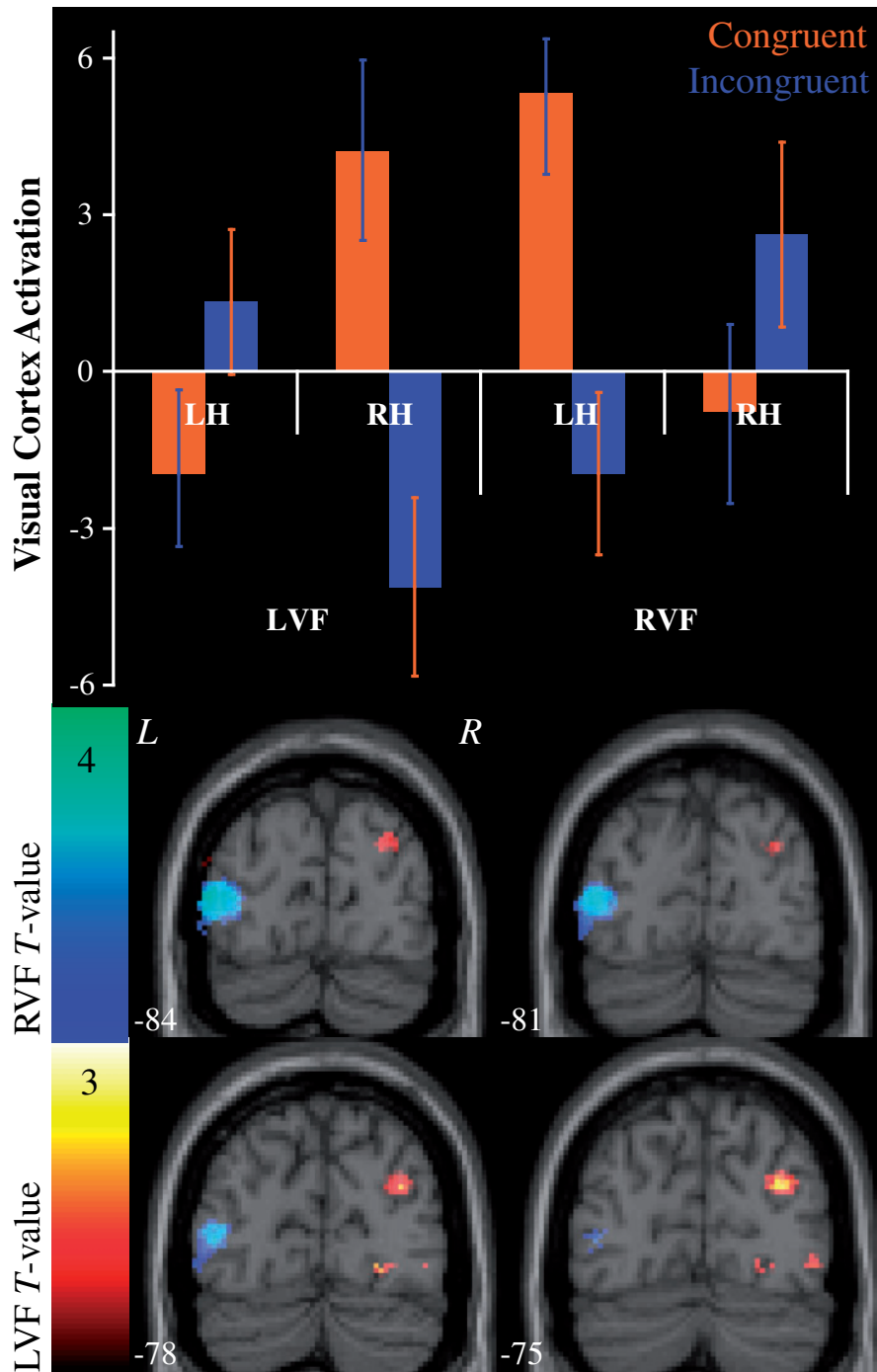


Fig. 2 As can be seen in the top panel, there was a cued visual field \times hemisphere \times congruency interaction where congruent trials increased visual cortical processing in the hemisphere contralateral to the backward masked fearful face cued visual field. In particular, LVF congruent, relative to incongruent, trials revealed greater activity in the right SOG, FG, and the lateral occipital complex (hot colors). RVF congruent, relative to incongruent, enhanced activation was limited to the left MOG (cool colors).

result adds to neuroimaging research on unmasked emotional and non-emotional attention cues (Di Russo *et al.*, 2003; Pourtois *et al.*, 2004, 2006; Fu *et al.*, 2005; Natale *et al.*, 2006) by demonstrating that attention cues, whether unmasked or masked, facilitate the processing of visual stimuli within the 'site' of attentional capture. On the other hand, the posterior parietal cortex has been implicated in the orienting

of spatial attention to non-emotional cues (Kim *et al.*, 1999; Peelen *et al.*, 2004), while the amygdala appears to mediate the attentional response to masked fearful faces (Carlson *et al.*, 2009). Although the structures that mediate the orienting of attention to a particular type of attentional cue may differ, the modulation of visual cortical processing appears to be consistent across most forms of visuospatial attention.

While we did not find a behavioral effect for RVF trials, the fMRI data unexpectedly revealed that RVF congruent, relative to incongruent, trials enhanced contralateral activity in the left MOG. Consequently, the lack of facilitated RTs to masked RVF fearful face congruent trials may reflect the absence of a coordinated visuomotor response, rather than a pure attentional neglect to RVF faces *per se*. In contrast, the contralateral enhancement of the right SOG (a structure in the dorsal visual stream, which is thought to be important in integrating visual and motor processing) during LVF masked fearful face trials may have contributed to a primed visuomotor response, which resulted in the facilitation of behavioral RTs. Furthermore, while RVF congruent trials modulated contralateral left MOG this modulation was not as distributed as the contralateral modulation of right SOG, FG and LOC by LVF congruent targets, which may indicate that a more distributed facilitation in contralateral occipital cortex mediates behavioral enhancements in spatial attention.

Although we report new findings that backward masked fearful face-elicited spatial attention modulates contralateral visual cortical processing for subsequently presented congruent targets, future exploration of this effect is needed. Specifically, future research exploiting retinotopic mapping techniques, which allow for finer spatial resolution of the visual cortical regions, would be useful in determining more precisely where in the visual cortical processing stream this modulation is occurring. Additionally, research focusing on the nature of the target stimulus and how different types of visual stimuli within the 'spotlight of attention' are influenced is needed. For example, the amygdala appears to preferentially respond to the low spatial frequency features of fearful faces (Vuilleumier *et al.*, 2003) and appears to mediate the attentional response to crude fearful faces (Carlson *et al.*, 2009). Given this, one might expect low spatial frequency stimuli (i.e. targets) to receive greater contralateral attention modulation in visual cortex than high spatial visual stimuli. Additionally, one might expect face targets to receive preferential fearful face-elicited attentional modulation than non-face targets, especially in face processing regions such as the fusiform face area and STS (Haxby *et al.*, 2000). It makes intuitive sense for threat-elicited modulations of visual cortical processing to preferentially modulate the features or representations eliciting this attentional response (e.g. the low spatial frequency features of a fearful face); however, this aspect of threat-elicited attention modulation has yet to be explored.

It should be noted that while we were unable to separate out the hemodynamic response function for faces and targets (i.e. we did not jitter between these events), our analysis method enables us to conclude that our results reflect the processing of the spatially congruent fearful face-dot pair. That is, in a congruent *vs* incongruent contrast the only difference is in the location of the target dot, while the location of the fearful face is consistent. Furthermore, we

implemented a masking procedure that was designed to eliminate processing specific to the target dot ('Results' section). Thus, the spatially congruent fearful face-dot pair rather than the dot or fearful face alone should drive differences in the BOLD signal between these trial types. Nevertheless, future research should attempt to replicate our findings and to disentangle the BOLD signal for the processing of the target dot and fearful face.

In sum, earlier work (Carlson *et al.*, 2009) has demonstrated that the amygdala, ACC and contralateral visual cortex are involved in directing or orienting attention to crude threat signals. Here, we provide new evidence that visual cortical processing of visual stimuli occurring within the masked fearful face-elicited 'spotlight of attention' is enhanced. In particular, LVF congruent relative to incongruent trials significantly enhanced activity in the right SOG, FG and LOC, while RVF congruent, relative to incongruent, trials enhanced left MOG activation. This more distributed modulation of brain activity for LVF (compared to RVF) trials may explain the observed behavioral facilitation in the LVF, but not RVF. Additionally, the contralateral enhancement of the right SOG during masked LVF fearful face trials may have contributed to a primed visuomotor response, which facilitated RTs.

REFERENCES

- Adolphs, R. (2004). Emotional vision. *Nature Neuroscience*, 7(11), 1167–8.
- Armony, J.L., Dolan, R.J. (2002). Modulation of spatial attention by fear-conditioned stimuli: an event-related fMRI study. *Neuropsychologia*, 40(7), 817–26.
- Carlson, J.M., Reinke, K.S. (2008). Masked fearful faces modulate the orienting of covert spatial attention. *Emotion*, 8(4), 522–9.
- Carlson, J.M., Reinke, K.S. (2010). Spatial attention-related modulation of the N170 by backward masked fearful faces. *Brain and Cognition*, 73, 20–27.
- Carlson, J.M., Reinke, K.S., Habib, R. (2009). A left amygdala mediated network for rapid orienting to masked fearful faces. *Neuropsychologia*, 47(5), 1386–9.
- Cooper, R.M., Langton, S.R. (2006). Attentional bias to angry faces using the dot-probe task? It depends when you look for it. *Behaviour Research and Therapy*, 44(9), 1321–9.
- Di Russo, F., Martinez, A., Hillyard, S.A. (2003). Source analysis of event-related cortical activity during visuo-spatial attention. *Cerebral Cortex*, 13(5), 486–99.
- Fox, E. (2002). Processing emotional facial expressions: the role of anxiety and awareness. *Cognitive, Affective and Behavioral Neuroscience*, 2(1), 52–63.
- Fu, S., Greenwood, P.M., Parasuraman, R. (2005). Brain mechanisms of involuntary visuospatial attention: an event-related potential study. *Human Brain Mapping*, 25(4), 378–390.
- Gur, R.C., Sara, R., Hagendoorn, M., et al. (2002). A method for obtaining 3-dimensional facial expressions and its standardization for use in neurocognitive studies. *Journal of Neuroscience Methods*, 115(2), 137–43.
- Haxby, J.V., Hoffman, E.A., Gobbini, M.I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Science*, 4(6), 223–33.
- Holland, P.C., Gallagher, M. (1999). Amygdala circuitry in attentional and representational processes. *Trends in Cognitive Science*, 3(2), 65–73.
- Jiang, Y., He, S. (2006). Cortical responses to invisible faces: dissociating subsystems for facial-information processing. *Current Biology*, 16(20), 2023–9.

- Kim, Y.H., Gitelman, D.R., Nobre, A.C., Parrish, T.B., LaBar, K.S., Mesulam, M.M. (1999). The large-scale neural network for spatial attention displays multifunctional overlap but differential asymmetry. *Neuroimage*, 9(3), 269–77.
- Liddell, B.J., Brown, K.J., Kemp, A.H., et al. (2005). A direct brainstem-amygdala-cortical ‘alarm’ system for subliminal signals of fear. *Neuroimage*, 24(1), 235–43.
- MacLeod, C., Mathews, A. (1988). Anxiety and the allocation of attention to threat. *The Quarterly Journal Of Experimental Psychology A, Human Experimental Psychology*, 40(4), 653–70.
- Mogg, K., Bradley, B.P. (1999). Orienting of attention to threatening facial expressions presented under conditions of restricted awareness. *Cognition and Emotion*, 13(6), 713–40.
- Mogg, K., Bradley, B.P. (2002). Selective orienting of attention to masked threat faces in social anxiety. *Behaviour Research and Therapy*, 40(12), 1403–14.
- Morris, J.S., Ohman, A., Dolan, R.J. (1998). Conscious and unconscious emotional learning in the human amygdala. *Nature*, 393(6684), 467–70.
- Morris, J.S., Ohman, A., Dolan, R.J. (1999). A subcortical pathway to the right amygdala mediating “unseen” fear. *Proceedings of the National Academy of Sciences of the United States of America*, 96(4), 1680–5.
- Natale, E., Marzi, C.A., Girelli, M., Pavone, E.F., Pollmann, S. (2006). ERP and fMRI correlates of endogenous and exogenous focusing of visual-spatial attention. *The European Journal of Neuroscience*, 23(9), 2511–21.
- Ohman, A., Flykt, A., Esteves, F. (2001). Emotion drives attention: detecting the snake in the grass. *Journal of Experimental Psychology General*, 130(3), 466–78.
- Peelen, M.V., Heslenfeld, D.J., Theeuwes, J. (2004). Endogenous and exogenous attention shifts are mediated by the same large-scale neural network. *Neuroimage*, 22(2), 822–30.
- Phelps, E.A., Ling, S., Carrasco, M. (2006). Emotion facilitates perception and potentiates the perceptual benefits of attention. *Psychological Science*, 17(4), 292–9.
- Posner, M.I. (1980). Orienting of attention. *The Quarterly Journal of Experimental Psychology*, 32(1), 3–25.
- Pourtois, G., Grandjean, D., Sander, D., Vuilleumier, P. (2004). Electrophysiological correlates of rapid spatial orienting towards fearful faces. *Cerebral Cortex*, 14(6), 619–33.
- Pourtois, G., Schwartz, S., Seghier, M.L., Lazeyras, F., Vuilleumier, P. (2006). Neural systems for orienting attention to the location of threat signals: an event-related fMRI study. *Neuroimage*, 31(2), 920–33.
- Sarter, M., Bruno, J.P., Givens, B. (2003). Attentional functions of cortical cholinergic inputs: what does it mean for learning and memory? *Neurobiology of Learning and Memory*, 80(3), 245–56.
- Vuilleumier, P., Armony, J.L., Driver, J., Dolan, R.J. (2003). Distinct spatial frequency sensitivities for processing faces and emotional expressions. *Nature Neuroscience*, 6(6), 624–31.
- Vuilleumier, P., Richardson, M.P., Armony, J.L., Driver, J., Dolan, R.J. (2004). Distant influences of amygdala lesion on visual cortical activation during emotional face processing. *Nature Neuroscience*, 7(11), 1271–8.
- Walter, B., Blecker, C., Kirsch, P., et al. (2003, June 19–22). *MARINA: An easy to use tool for the creation of MAsks for Region of INterest Analyses*. Paper presented at the 9th International Conference on Functional Mapping of the Human Brain, New York, NY.
- 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 Neuroscience*, 18(1), 411–18.
- Williams, L.M., Liddell, B.J., Kemp, A.H., et al. (2006). Amygdala-prefrontal dissociation of subliminal and supraliminal fear. *Human Brain Mapping*, 27(8), 652–61.