

Brain Responses to Biological Relevance

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Abstract

■ This study examines whether orienting attention to biologically based social cues engages neural mechanisms distinct from those engaged by orienting to nonbiologically based non-social cues. Participants viewed a perceptually ambiguous stimulus presented centrally while performing a target detection task. By having participants alternate between viewing this stimulus as an eye in profile or an arrowhead, we were able to directly compare the neural mechanisms of attentional orienting to social and nonsocial cues while holding the physical stimulus constant. The functional magnetic resonance imaging results indicated that attentional orienting to both eye gaze and arrow cues engaged extensive dorsal and ventral frontoparietal networks. Eye gaze cues, however, more vigorously engaged two regions in the ventral frontal cortex associated with attentional reorienting to salient or meaningful stimuli,

as well as lateral occipital regions. An event-related potential study demonstrated that this enhanced occipital response was attributable to a higher-amplitude sensory gain effect for targets appearing at locations cued by eye gaze than for those cued by an arrowhead. These results endorse the hypothesis that differences in attention to social and nonsocial cues are quantitative rather than qualitative, running counter to current models that assume enhanced processing for social stimuli reflects the involvement of a unique network of brain regions. An intriguing implication of the present study is the possibility that our ability to orient volitionally and reflexively to socially irrelevant stimuli, including arrowheads, may have arisen as a useful by-product of a system that developed first, and foremost, to promote social orienting to stimuli that are biologically relevant. ■

INTRODUCTION

Most of us have had the experience of trying to carry on a conversation with someone who looks away distractedly. When this happens, it is often difficult to continue the conversation because your attention is diverted to whatever your conversation partner is looking at. Far from being anecdotal, this phenomenon—that one's visual attention can be directed reflexively to locations indicated by another's eye gaze—is well documented (Frischen & Tipper, 2004; Langton & Bruce, 1999; Friesen & Kingstone, 1998). These studies have given rise to the theoretical claim that eye gaze is a particularly powerful, “special” cue for visuospatial attention. Although there is evidence that contextual information such as head orientation and body movements modulates attention to gaze direction (Langton, Watt, & Bruce, 2000), the importance of the eyes themselves as a social cue is hard to deny.

The special status of eye gaze as a cue for spatial attention may owe, at least in part, to specialized neural systems for processing eye gaze information. The superior temporal sulcus (STS) has been implicated in numerous studies as a region specialized for processing eye

gaze (Kingstone, Tipper, Ristic, & Ngan, 2004; Allison, Puce, & McCarthy, 2000; Hoffman & Haxby, 2000; Perrett et al., 1985). More recent neuroimaging work suggests that specific regions within the STS may be specialized not only for the processing of eye gaze information but also for the processing of several forms of biological motion, including mouth, eye, and hand movements (Pelphrey & Morris, 2006; Pelphrey, Morris, Michelich, Allison, & McCarthy, 2005). Although there is ongoing debate regarding the specificity of STS functionality, there is growing consensus that the STS plays an integral role in the perception of social cues in particular, rather than simply any directional stimuli (Hooker et al., 2003). Nevertheless, although the STS is an important player in the *perceptual* processing of eye gaze, whether there are neural systems specialized for orienting attention to this biologically based social cue remains an open question.

The use of biologically based cues in shifting visual attention, what we will call social attention, provides information regarding one's surroundings even in the absence of direct visual perception. The social extension of one's own attentional and perceptual reach would have constituted a beneficial cognitive adaptation in an ancestral environment rife with intergroup conflicts and predators with far greater strength and speed. This evolutionary argument for specialized mechanisms mediating social attention is supported by the finding that

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monkeys and humans may share a homologous neural mechanism for social attention (Deaner & Platt, 2003). The present study examines whether specialized neural mechanisms facilitate the orienting of attention to social cues in humans. Specifically, we asked whether visuospatial attentional orienting to directional biological cues (eyes) engages neural mechanisms distinct from those engaged by orienting to directional nonbiological cues (arrows). We will refer to the former as social cues, and the latter as nonsocial cues.

One possibility is that orienting to social cues does utilize specialized neural modules. In patients with visuospatial neglect, for example, gaze direction cues can induce shifts in attention to regions of space to which these patients cannot otherwise attend (Vuilleumier, 2002). In addition, although both hemispheres in a split-brain patient were recruited in orienting attention to arrow stimuli, only the predominant face-processing hemisphere was engaged while orienting attention to eye gaze stimuli (Kingstone, Friesen, & Gazzaniga, 2000). Consistent with these patient studies, one recent functional magnetic resonance imaging (fMRI) study reported that although arrow cues engaged areas of the frontal and parietal cortex typically involved in volitional orienting, gaze cues did not (Hietanen, Nummenmaa, Nyman, Parkkola, & Hämäläinen, 2006). These results suggest that attentional orienting to eye gaze may utilize neural mechanisms distinct from those needed for orienting in response to nonsocial stimuli, such as arrows. A second possibility, however, is that the same neural mechanisms subserve attentional orienting to any meaningful or symbolic stimulus. This possibility is consistent with behavioral studies demonstrating equivalent orienting to centrally presented eyes and arrows (Quadflieg, Mason, & Macrae, 2004; Ristic, Friesen, & Kingstone, 2002; Tipples, 2002).

To test between these competing hypotheses, we asked participants to view a perceptually ambiguous object that could be interpreted either as an eye in profile (Figure 1, looking to the right), or an arrowhead (Figure 1, pointing to the left). By instructing participants to alternate between viewing this object as an eye or an arrow while they underwent fMRI scanning, we were able to compare the neural mechanisms of attentional orienting to social and



Figure 1. Ambiguous cue stimulus. Participants were instructed to perceive this stimulus as either an arrow (e.g., pointing the left) or as an eye in profile (e.g., looking to the right). How the participants viewed this ambiguous shape was alternated via instructions. This cue stimulus was presented at fixation at the beginning of each trial and varied in its gazing/pointing direction from trial-to-trial.

nonsocial cues while holding the physical cue stimulus constant. If there are specialized neural modules for orienting to social cues such as eye gaze, then we would expect to find greater blood oxygenation level-dependent (BOLD) activity in these regions when viewing the ambiguous object as an eye relative to when viewing that same stimulus as an arrow. If, on the other hand, both eye gaze and arrow cues utilize the same orienting network, we would expect both percepts to equally engage a fronto-parietal orienting network (Corbetta & Shulman, 2002).

EXPERIMENT 1

While undergoing fMRI scanning, participants viewed the centrally presented object as either an eye or an arrow. Periodically, we instructed participants to switch how they perceived the object. The results of a pilot study ensured that participants were able to maintain each percept with equal ease, and switch percepts effectively when to do so (and see Experiment 3 for direct behavioral evidence supporting these claims). Participants responded with a button press as quickly as possible when they saw an asterisk appear in the left or right periphery either 100 or 600 msec following the onset of the cue. Importantly, they could not predict the location of the target based on the central object, a fact about which they were informed. On half of the trials, the target appeared at the location to which the eye gazed or the arrow pointed (cued). On the other half of trials, the target appeared at the opposite location (uncued). Because participants could not predict the location of the target based on the central object, there was no explicit reason for participants to attend to one location or the other in response to the central cue stimulus. Shorter response latencies to targets appearing at the cued relative to the uncued location could therefore be interpreted as indicating a reflexive, or automatic, shift in visuospatial attention in the direction cued by the central object (Posner, 1980).

Methods

Participants

Eight neurologically healthy, right-handed participants (mean age = 23.75 years, 3 women) from the University of British Columbia took part in the study with written consent. All participants had normal or corrected-to-normal vision. Experimental procedures were approved by the University of British Columbia Clinical Research Ethics Board. Participants were remunerated with structural images of their brains on CD.

Stimuli and Task

Visual stimuli were presented to participants via rear projection through the scanner bore onto a mirror, which reflected the image to the participant. Experimental

stimuli consisted of a central fixation point, centrally presented cues and peripherally presented response targets. The cue was always presented at fixation. The response target was simply an asterisk presented to the left or the right of center. All stimuli were black shapes presented on a white background.

The task was to fixate centrally on a small point, and to actively perceive the cue stimulus according to instruction (either as an eye or as an arrow). In addition, participants were told to press a response button as quickly and as accurately as possible when they saw the target appear. Importantly, the direction of the reflexive attentional shift induced by the cue should vary depending on whether it is being viewed as an eye or as an arrow.

Procedure

At the beginning of the testing session, participants were instructed to see the cue stimulus as either an eye or as an arrow. They were not given any indication at the outset that the cue stimulus could be viewed any other way. Halfway through the testing session, however, participants were instructed to switch their perceptual set in order to see the cue as the alternative object; successful perceptual switching could be confirmed via the pattern of response times (RTs) to the targets as a function of their visual field and the orienting direction of the percept (see Experiment 3). The testing session was divided into four functional scanning runs, including two consecutive runs viewing the cue as an eye, and two consecutive runs viewing the cue as an arrow. Whether the cue was first viewed as an eye or as an arrow was counterbalanced across participants. In all cases, participants were informed that cue direction did not reliably predict the target location.

Each scanning run consisted of 93 trials, which included 64 cue–target trials (in which both a cue and a target occurred), 20 catch trials (in which a cue was not followed by a target), and 9 fixation-only trials (in which neither a cue nor a target occurred) that lasted a duration of either one, two, or three TRs.

Each cue–target and catch trial began with a 750-msec blank screen. A small fixation point would then appear for 750 msec, at which time it would be replaced by the cue stimulus. For cue–target trials, either 100 or 600 msec following the onset of the cue, the target would appear on the left or the right of the cue. The target stayed on the screen for the remainder of the trial, which lasted for 2250 msec, irrespective of when the response was made. The screen then blanked for a 750 msec intertrial interval (ITI). Half of all cue–target trials were cued trials, in which the target would appear at the gazed-at or pointed-at location, and the other half of trials were uncued trials, in which the target would appear at the opposite location. An equal number of left gazing/pointing and right gazing/pointing cues were presented randomly in each experimental condition.

fMRI Acquisition and Image Processing

fMRI data were collected on a research-dedicated Phillips 3-T system fitted with a SENSE head coil. Conventional spin-echo, T1-weighted sagittal localizers were used to view the positioning of the participant's head and to set the functional image volumes to be acquired in line with the AC–PC plane. Functional image volumes were collected with an echo-planar imaging gradient-echo pulse sequence (TR = 2000 msec, TE = 30 msec, 90° flip angle, FOV = 240 × 240 mm, 128 × 128 matrix, 62.5 kHz bandwidth, 3.00 × 3.00 mm final measured in-plane resolution, 3.00 mm slice thickness, 1.00 mm slice gap, 36 interleaved transverse slices), which is sensitive to BOLD contrast.

A transistor-transistor logic (TTL) pulse from the scanner started the scanning run such that the scanner and the visual presentation of stimuli were synched for timing. The run consisted of four initial dummy scans (to allow time to achieve steady-state magnetization) and 166 functional scans. After participants completed four functional runs, a high-resolution T1-weighted structural image was acquired with a 3-D gradient-echo pulse sequence (TR = shortest, TE = shortest, 8° flip angle, FOV 256 × 256 mm, 256 × 256 matrix, 1.00 × 1.00 mm in-plane resolution, 1.00 mm slice thickness, 170 slices).

The task was programmed and presented on a personal computer running Presentation software (Neurobehavioral Systems, San Francisco, CA). An event-related fMRI design was used, which allowed the pseudorandom intermixed presentation of cued, uncued, and catch trials, as well as fixation-only trials. Responses were collected on a fiber-optic MR-compatible response device (Lightwave Medical, Vancouver, BC). Stimulus and response timing was recorded in a log file that was later analyzed to generate behavioral RTs.

Functional images were reconstructed off-line. Statistical Parametric Mapping software (SPM2, Wellcome Institute of Cognitive Neurology, London, UK) was used for image orientation, motion correction, and spatial normalization into modified Talairach anatomical space. A low-pass filter (high frequency cutoff = 6.25 sec) implemented in MATLAB (The Mathworks, Natick, MA) was applied to the data prior to statistical interrogation in order to eliminate high-frequency noise confounds not associated with the BOLD effect.

Statistical Analyses

SPM2 was used to construct a 2 × 2 × 3 fixed-effects general linear model for analyzing the group-wise data, with percept (eye vs. arrow), cue direction (left vs. right), and cueing (cued vs. uncued vs. catch) as factors. Each condition was modeled as a set of events time-locked to the onset of the cue and convolved with a synthetic hemodynamic response function. Temporal derivative regressors were also included in the model. Specific BOLD effects of interest were examined by

creating linear contrasts of the parameter estimates for each condition. The linear contrasts resulted in a t statistic for each voxel (unit of fMRI spatial resolution), which could then be assessed for statistical significance across the whole brain, thresholded at $p < .05$, corrected for multiple comparisons.

In order to identify the cortical networks associated with reflexive attentional orienting to centrally presented spatially nonpredictive cues, we looked at the BOLD response to eye cues and arrow cues independently. In order to ascertain whether there are any differences in attentional networks for orienting to eyes as opposed to arrows, we looked at the relative BOLD effects (i.e., Eye cues > Arrow cues).

Results

Behavior

Table 1 shows mean RTs. Regardless of whether the cue was perceived as an eye or an arrow, responses to cued targets were faster than responses to uncued targets. This behavioral cueing effect did not vary as a function of stimulus-onset asynchrony (SOA) or percept order. An ANOVA with percept (eye vs. arrow), cueing (cued vs. uncued), and SOA (100 msec vs. 600 msec) as within-subject factors, and percept order (eye first vs. arrow first) as a between-subject factor established the statistical significance of these findings. The main effect of percept was not significant [$F(1, 7) = 1.5, p > .05$], indicating no overall difference in RTs between eye and arrow percepts. The main effect of cueing was significant [$F(1, 7) = 29.5, p < .05$], as was the main effect of SOA [$F(1, 7) = 10.0, p < .05$]. Neither the cueing factor nor the SOA factor interacted with any other factors (all p s > .05). Given that both percepts gave rise to equivalent

Table 1. Response Time Data for Experiment 1 (fMRI)

Cue Type	SOA			
	100 msec		600 msec	
	Mean	SE	Mean	SE
<i>Eye Gaze</i>				
Cued	428.78	28.79	363.55	15.75
Uncued	460.97	34.62	381.85	15.96
<i>Arrow</i>				
Cued	417.37	31.62	348.65	18.84
Uncued	427.91	38.67	374.78	19.38

The results indicate faster responses for cued relative to uncued targets at both short and long cue–target intervals, regardless of whether the cue was perceived as an arrow or as an eye. These equivalent attentional orienting effects occurred despite the fact that participants were assured that the cue did not reliably predict the location of the impending target.

reflexive attentional orienting, the question then was whether these two types of attentional cues would engage distinct cortical mechanisms.

Functional Magnetic Resonance Imaging

We conducted a two-part analysis of the fMRI data. First, we looked at BOLD responses to the eye gaze and arrow cues independently. This allowed us to identify the cortical regions subserving attentional orienting to each type of cue. Second, we directly compared BOLD responses to eye and arrow cues in order to identify regions having a differential response to the two types of cue. Both analyses were time-locked to the onset of the cue stimulus, and included cued trials only.

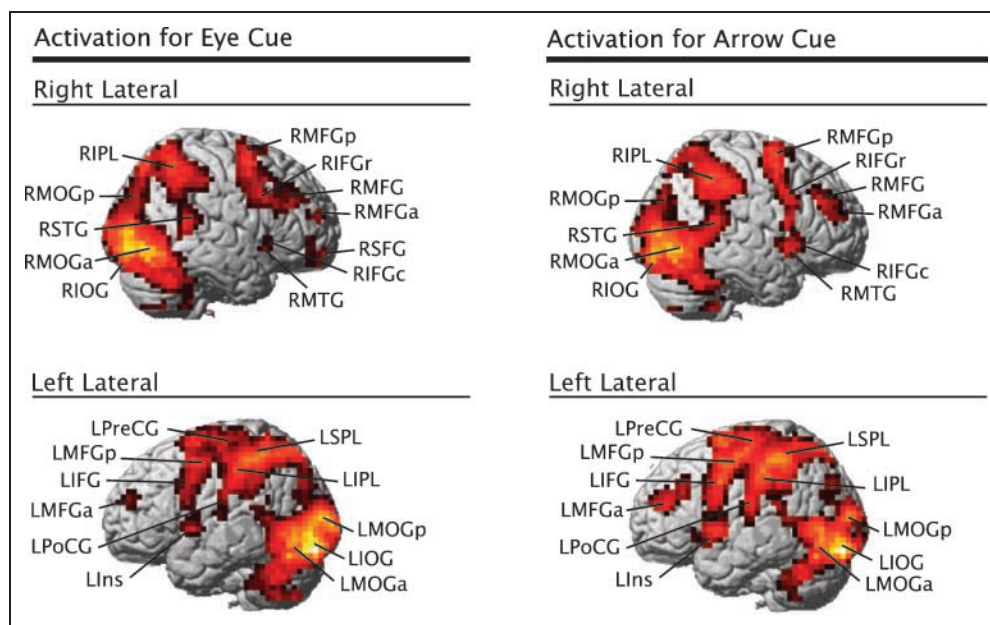
The cortical regions in which the BOLD response increased significantly ($p < .05$, corrected) with the presentation of the central object are shown in Figure 2. The BOLD responses to eye and arrow cues were similar. For both cue types, posterior regions of activity included large clusters in the bilateral intraparietal sulcus, superior parietal lobule, and the temporal–parietal junction, including the inferior parietal lobule, and the superior temporal gyrus (STG). In more anterior brain regions, there were significant clusters in the bilateral dorsal frontal cortex, including the middle frontal and superior frontal gyri. Bilateral anterior clusters were also found more ventrally in the STG. Prominent BOLD responses in the occipital cortex, extending into posterior ventral temporal regions, were also observed. Table 2 provides coordinates and t values for some of the local maxima in each of these regions.

Although orienting to eye and arrow cues activated largely similar cortical regions, we were interested in directly probing the question of whether any cortical regions were uniquely associated with attentional orienting to eye gaze cues. The results of the relative BOLD contrast ($p < .05$, corrected) showing regions responding more vigorously to eye cues than to arrow cues are depicted in Figure 3. Four clusters were identified, including two clusters in the bilateral middle occipital gyri, a cluster on the ventral surface of the right medial frontal gyrus, and a cluster in the right inferior precentral gyrus. Table 3 lists coordinates and t values for the most highly activated voxel in each of these clusters. When we conducted the reverse contrast, we found no regions with a significantly greater BOLD response for arrows than for eyes.

EXPERIMENT 2

The finding that the lateral occipital cortex showed a larger BOLD response for eye gaze than for arrow cues was interesting given that the physical stimulus for each type of cue was identical. One possible explanation for the enhanced occipital activation is that an eye gaze cue may be particularly effective for enhancing visual sensory

Figure 2. Attentional orienting network. Independent analyses of the BOLD response to eye gaze and arrow cues are shown here. A general linear model approach (see Experiment 1 Methods) was used to identify BOLD activity specific to the processing of the cue. Activation maps, representing voxels with a t statistic greater than 4.63 ($p < .05$, corrected), are overlaid on the SPM2 single-subject rendered brain template (MNI). Largely the same network was activated while orienting attention to eye gaze and arrow stimuli. R = right hemisphere, L = left hemisphere; r = rostral; c = caudal; a = anterior; p = posterior; IFG = inferior frontal gyrus; MFG = middle frontal gyrus; SFG = superior frontal gyrus; PreCG = precentral gyrus; Ins = insula; IPL = inferior parietal lobule; PoCG = postcentral gyrus; SPL = superior parietal lobule; STG = superior temporal gyrus; MTG = middle temporal gyrus; MOG = middle occipital gyrus; IOG = inferior occipital gyrus.



processing for stimuli appearing at gazed-at locations (Hopfinger & Ries, 2005). That is, although both eye and arrow cues induce reflexive shifts in spatial attention, and utilize largely the same cortical regions to do so, eye gaze cues may be associated with a larger visual sensory gain effect in the lateral occipital cortex than arrow cues. In order to test this possibility, a second experiment was conducted with an independent group of participants using event-related potentials (ERPs).

An attention-related sensory gain effect is characterized by a larger-amplitude P1 ERP component in response to the onset of a visual stimulus when that stimulus is presented at an attended (cued) location than when it is presented at an unattended (uncued) location (cf. Mangun & Hillyard, 1991). If indeed the more robust BOLD response in the occipital cortex was caused by a larger sensory gain effect, then we would expect to find a larger difference in P1 amplitudes for cued and uncued targets when the attention-orienting stimulus is perceived as an eye than when it is perceived as an arrow. The stimuli and task used in Experiment 2 were identical to those employed in Experiment 1, with the exception of some changes made to the timing of stimulus presentation in order to facilitate ERP data collection.

Methods

Participants

Thirteen neurologically healthy, right-handed participants from the University of British Columbia took part in the study with written consent. The data from two participants were discarded due to technical problems leading to excessive noise in the electroencephalogram

(EEG), and a failure to evoke a distinguishable P1 ERP component. Of the remaining 11 participants, 5 were women, and the mean age was 20.55 years. All participants had normal or corrected-to-normal vision. Experimental procedures were approved by the University of British Columbia Behavioral Research Ethics Board. Participants were remunerated with 10 dollars per hour of their time.

Stimuli and Task

The stimuli and task employed were nearly identical to those used in Experiment 1. On most trials, a cue stimulus was presented, followed shortly by an asterisk target. The directionality of the cue did not predict the location of the target. There were a few changes made in order to accommodate the requirements of an ERP study. The display was presented on a 17-inch CRT monitor at a viewing distance of approximately 100 cm. In addition, the timing of the stimulus presentation differed from that used in Experiment 1. The interval between the cue and the target was randomly selected on each trial from a rectangular distribution between 500 and 700 msec. A long intertrial interval, randomly varied between 2400 and 2600 msec, was added for the purpose of obtaining accurate baseline measures for ERPs.

Procedure

Participants were fitted with an elastic cap containing an array of 31 tin electrodes (Electro-Cap International, Eaton, OH). Half of the participants were instructed to perceive the ambiguous cue shape as an arrow; the

Table 2. BOLD Cluster Maxima for Eye Gaze and Arrow Cues, $p < .05$, Corrected for Multiple Comparisons

Region	Eye Gaze Cue				Arrow Cue			
	<i>x, y, z</i> Coordinates (mm)			<i>t</i> -Score	<i>x, y, z</i> Coordinates (mm)			<i>t</i> -Score
<i>Frontal</i>								
RIFGr	52	12	32	6.42	52	12	32	7.55
RIFGc	48	16	-4	5.32	48	16	-4	8.05
RMFGa	36	56	16	6.86	48	48	16	5.76
RMFG	52	36	28	7.34	52	36	28	4.78
RMFGp	36	0	64	10.03	36	0	64	10.97
RSFG	20	56	-16	7.41	-	-	-	$p > .05$
LIFGr	-56	12	28	8.21	-56	12	28	11.01
LIFGc	-56	12	-4	4.68	-48	12	-4	5.05
LMFGa	-36	52	24	6.25	-40	44	20	8.52
LMFGp	-32	-4	48	10.89	-36	-4	48	12.31
LPreCG	-32	-20	68	8.30	-32	-20	68	12.08
LIns	-40	8	0	6.46	-40	8	0	8.41
<i>Parietal</i>								
RIPL	24	-76	56	11.43	40	-44	44	10.89
LPoCG	-60	-16	24	6.41	-60	16	24	8.73
LSPL	-24	-64	56	12.87	-24	-64	56	7.88
LIPL	-28	-40	44	12.06	-44	-32	40	12.51
<i>Temporal</i>								
RSTG	48	-40	8	7.75	48	-40	8	4.88
RMTG	52	16	-4	5.92	52	16	-4	6.53
<i>Occipital</i>								
RMOGp	32	-92	12	11.29	32	-92	12	10.06
RMOGa	48	-72	-8	14.72	48	-72	-8	14.63
RIOG	44	-76	8	15.88	44	-76	8	6.41
LMOGp	-32	-92	8	14.94	-32	-92	8	11.74
LMOGa	-44	-76	-12	14.10	-44	-76	-12	13.77
LIOG	-44	-84	-8	16.14	-44	-84	-8	10.69

Regions listed are represented in Figure 2. R = right hemisphere; L = left hemisphere; r = rostral; c = caudal; a = anterior; p = posterior; IFG = inferior frontal gyrus; MFG = middle frontal gyrus; SFG = superior frontal gyrus; PreCG = precentral gyrus; Ins = insula; IPL = inferior parietal lobule; PoCG = postcentral gyrus; SPL = superior parietal lobule; STG = superior temporal gyrus; MTG = middle temporal gyrus; MOG = middle occipital gyrus; IOG = inferior occipital gyrus.

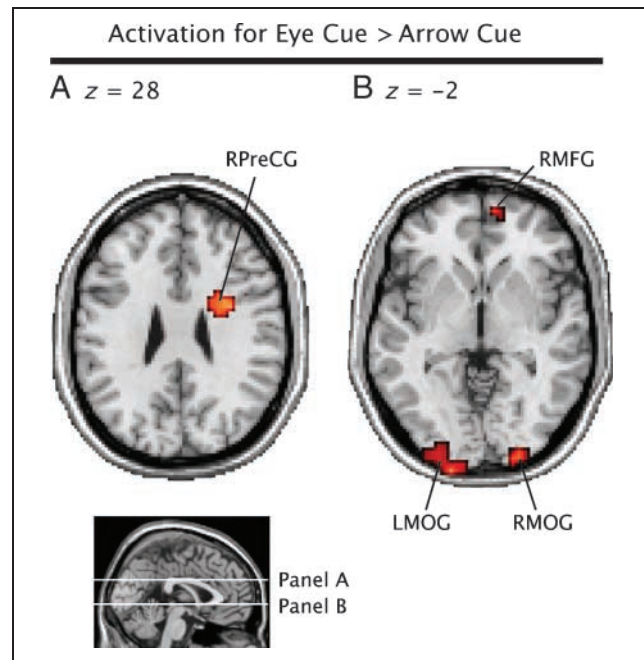


Figure 3. Regions preferentially engaged by the eye gaze cue. Regions exhibiting a large BOLD response ($t > 4.63$, $p < .05$, corrected) for the eye gaze percept than the arrow percept are shown here. Activation maps are overlaid on two slices of the SPM single-subject T1 image template (MNI). Four clusters responded more vigorously while attending to the eye gaze cue than while attending to the arrow cue. Panel A shows a cluster in the right inferior precentral gyrus. Panel B shows three clusters, one on the ventral surface of the right middle frontal gyrus, and two located in bilateral middle occipital gyri. R = right hemisphere; L = left hemisphere; MFG = middle frontal gyrus; PreCG = precentral gyrus; MOG = middle occipital gyrus.

Table 3. BOLD Cluster Maxima for Eye Gaze Cue > Arrow Cue Statistical Contrast

Region	Eye Gaze > Arrow Cue			<i>t</i> -Score
	<i>x, y, z</i> Coordinates (mm)			
<i>Frontal</i>				
RMFG	16	60	-4	5.57
RPreCG	36	0	28	7.18
<i>Occipital</i>				
RMOG	28	-100	-4	6.27
LMOG	-24	-100	4	5.14

Data reported here surpass the statistical threshold of $p < .05$, corrected for multiple comparisons. Regions listed are represented in Figure 3. R = right hemisphere; L = left hemisphere; MFG = middle frontal gyrus; PreCG = precentral gyrus; MOG = middle occipital gyrus.

other half were instructed to see it as an eye. After 10 trial blocks, participants were then instructed to see the cue stimulus as the other possible shape, and another 10 blocks were run. Each block lasted approximately 4 min, and consisted of 30 trials, including 28 cue–target trials, and 2 catch trials, in which no target occurred.

EEG data were collected from 24 scalp electrodes sites (FP1, FP2, Fz, F7, F8, Cz, C3, C4, T3, T4, P1, P2, Pz, P5, P6, PO1, PO2, Oz, OL, OR, P3, P4, T5, and T6) using a Grass Instruments Model 12 amplifier, referenced to the left mastoid. Three additional channels were recorded, one from the right mastoid (for off-line referencing of the data to the average of the two mastoid signals), one from a pair of electrodes mounted on the outer canthi of each eye (to record horizontal eye movements), and one from below the right eye (to record vertical eye movements and blink artifacts). EEG was amplified with a gain of 50,000 and a half-amplitude band pass of 0.1 to 30 Hz. Data were digitized at 256 Hz. Off-line, trials with eye movement artifacts were flagged and not included in any subsequent analysis. ERP waveforms were digitally re-referenced to the average of the left and right mastoids, and low-pass filtered (25.6 half-amplitude cutoff) prior to analysis. Peak amplitude measures for the P1 waveform were obtained by identifying the latency of the P1 peak for each condition of interest in the grand-averaged waveforms, and obtaining the voltage measure at that latency within each participant. All statistical analyses and waveform displays were conducted with a –100 to 0 msec prestimulus baseline.

Results

Behavior

Table 4 shows mean RTs and standard errors. The results indicate faster responses to cued relative to uncued targets, regardless of whether the cue was perceived as an eye or an arrow. Response time data were analyzed

Table 4. Response Time Data for Experiment 2 (ERP)

Cue Type	SOA	
	500–700 msec	
	Mean	SE
<i>Eye Gaze</i>		
Cued	276.31	14.67
Uncued	281.08	16.41
<i>Arrow</i>		
Cued	264.46	14.03
Uncued	276.44	14.99

The results show statistically equivalent attentional orienting effects for arrow and eye gaze percepts.

with an ANOVA, with percept (eye vs. arrow) and cueing (cued vs. uncued) as within-subject factors. The main effect of percept was not significant, [$F(1, 10) = 0.5, p > .05$], indicating no overall difference in RTs between eye and arrow percepts. There was a significant main effect of cueing [$F(1, 10) = 9.7, p < .05$]. The interaction of percept and cueing was not significant ($p > .05$), replicating the finding from Experiment 1 that eye and arrow cues induce equivalent attentional orienting effects.

Electrophysiology

ERP waveforms time-locked to target onset and averaged across participants are plotted in Figure 4. These data indicate that although both eye gaze and arrow cues produced behavioral cueing effects, an attention-related sensory gain effect was present only for eye gaze cues. Peak amplitude values in the P1 time window (Table 5) were submitted as the dependent variable in a $2 \times 2 \times 2 \times 2$ ANOVA with percept (eye vs. arrow), cueing (cued vs. uncued), visual Field of the target (left vs. right), and electrode (ipsilateral vs. contralateral) as within-subject factors. A significant three-way interaction between percept, cueing, and electrode [$F(1, 10) = 4.9, p = .05$] was followed up with simple effects analyses. These analyses indicated that the three-way interaction was driven by the presence of a significant sensory gain effect (greater P1 amplitudes for cued relative to uncued targets) for the eye gaze percept at electrode sites contralateral [$F(1, 50) = 4.6, p < .05$], but not ipsilateral [$F(1, 50) = 0.4, p > .05$], to the visual field of target presentation. There was no statistically significant sensory gain effect for the arrow percept at either contralateral [$F(1, 50) = 0.03, p > .05$] or ipsilateral [$F(1, 50) = 0.6, p > .05$] electrode sites. The results are consistent with the hypothesis that attentional orienting in response to an eye gaze cue is particularly effective at highlighting sensory information being processed at the gazed-at location.

EXPERIMENT 3

To date, all studies comparing the neural mechanisms of attentional orienting in response to eye gaze and arrow stimuli have used physically distinct stimuli. Although this is an obvious and unavoidable fact of comparing the orienting response to realistic depictions of distinct objects, it is important to note that it represents an inherent methodological confound for controlled investigations. Specifically, when comparing the orienting response to eye gaze and arrow cues with a study that utilizes physically distinct cues (e.g., Hietanen et al., 2006), one can never be certain of whether observed differences arise because of differences in the physical stimulus parameters, or due to differences in the meaningful (semantic) representations of those stimuli.

the remaining 16 participants, 9 were women, and the mean age was 21.32 years. Participants were assigned to one of two groups. The single-switch group was instructed to switch percepts only once, midway through testing, as in Experiments 1 and 2. The multi-switch group was instructed to switch percepts repeatedly throughout the experiment.

All participants had normal or corrected-to-normal vision. Experimental procedures were approved by the University of British Columbia Behavioral Research Ethics Board. Participants were remunerated with 10 dollars per hour of their time.

Stimuli, Task, and Procedure

The stimulus design and task were identical to that of Experiment 1, with the exception that half the participants were requested via an on-screen instruction to switch percepts six times throughout the experiment.

At the beginning of the testing session, participants in the single-switch group were instructed to perceive the cue stimulus as either an eye or as an arrow. They were not given any indication at the outset that the cue stimulus could be viewed any other way. Halfway through the testing session, however, these participants were instructed to switch their perceptual set in order to perceive the cue as the alternative object. Participants in the multi-switch group, however, were instructed from the outset that they would have to make perceptual switches, and to do so by following instructions presented on the screen at regular intervals throughout the experiment.

As in Experiment 1, the testing session was divided into four blocks of trials, each separated with a short break. For the single-switch group, there were two consecutive blocks viewing the cue as an eye, and two consecutive blocks viewing the cue as an arrow. For the multi-switch group, participants were instructed to switch percepts midway through each of the four blocks, as well as between most blocks. There were two consecutive eye gaze then arrow blocks, and two consecutive arrow then eye gaze blocks. Whether the cue was first viewed as an eye or as an arrow was counterbalanced across participants. This design resulted in six perceptual switches throughout the experiment with a switch order of either eye/arrow–eye/arrow–arrow/eye–arrow/eye or arrow/eye–arrow/eye–eye/arrow–eye/arrow. In all cases, participants were informed that cue direction did not reliably predict the target location.

Results

Mean RTs are presented in Table 6. The data were analyzed by a $2 \times 2 \times 2 \times 2$ ANOVA, with percept (eye vs. arrow), cueing (cued vs. uncued), and SOA (100 msec vs. 600 msec) as within-subject factors, and switch group (single-switch vs. multi-switch) as a between-subject factor. The results indicate statistically equivalent patterns

Table 6. Mean Response Times for Experiment 3

Group	Cue Type		SOA			
			100 msec		600 msec	
			Mean	SE	Mean	SE
Single-Switch	Eye Gaze	Cued	422.97	24.39	337.91	17.86
		Uncued	441.18	28.96	354.09	16.33
	Arrow	Cued	401.74	25.34	340.66	20.05
		Uncued	449.30	32.00	361.34	18.28
Multi-Switch	Eye Gaze	Cued	408.31	29.23	362.52	19.70
		Uncued	418.46	28.86	366.68	20.90
	Arrow	Cued	395.29	28.56	363.22	22.98
		Uncued	410.40	31.47	376.79	21.19

The results indicate no significant differences between groups, suggesting effective perceptual switching that does not produce any negative transfer effects. For both groups, responses were faster for cued relative to uncued targets at both short and long cue–target intervals, regardless of whether the cue was perceived as an arrow or as an eye.

of RTs associated with eye gaze and arrow percepts across both groups. There was no significant main effect of switch group [$F(1, 14) = 0.08, p > .05$], and no interaction of switch group with any other factor (all $ps > .05$). Overall, there was no main effect of percept [$F(1, 14) = 0.05, p > .05$]. There was, however, a significant main effect of cueing [$F(1, 14) = 21.4, p < .05$], as well as a main effect of SOA [$F(1, 14) = 44.0, p < .05$], but no Percept \times Cueing interaction [$F(1, 14) = 3.6, p > .05$]. Thus, in both the single-switch and multi-switch groups, participants were switching percepts appropriately, and the percepts triggered equivalent attentional orienting to the cued locations. These results support the conclusion that switching between interpreting the ambiguous cue stimulus as an eye or an arrow produces no negative carryover effects.

META-ANALYSIS: EXPERIMENTS 1 TO 3

Although the same pattern of results have been demonstrated in Experiments 1 to 3, one still might wish to argue that the relatively small sample sizes within each of these studies precluded the detection of differences between either the overall RTs within each percept condition, or the orienting effects generated by each percept. To maximize statistical power, we combined the data from Experiments 1 to 3 in a meta-analysis with a total of 35 participants.

Methods

As Experiment 2 included only one 600-msec SOA condition, the RTs from the 100-msec and 600-msec

SOA conditions within both Experiment 1 and Experiment 3 were averaged. A $2 \times 2 \times 4$ ANOVA was performed, with percept (eye vs. arrow) and cueing (cued vs. uncued) as within-subject factors, and experiment (Experiments 1, 2, 3) as a between-subject factor.

Results

Although the meta-analysis revealed a difference in overall RTs between experiments with a significant main effect of experiment [$F(3, 31) = 8.5, p < .05$], experiment did not interact with any other factor (all p s $> .05$). There was a significant cueing effect [$F(1, 31) = 55.5, p < .05$], indicating faster RTs for cued than for uncued targets. This cueing effect was equivalent for both eye gaze and arrow percepts, as indicated by the absence of a Percept \times Cueing interaction [$F(1, 31) = 2.2, p > .05$]. In addition, there was no main effect of percept [$F(1, 31) = 2.3, p > .05$], indicating equivalent RTs in both eye gaze and arrow percept conditions. This more powerful meta-analysis converges with, and reinforces, the conclusion that participants resolve and maintain eye and arrow cue percepts with equal ease and efficiency, and that these percepts induce behaviorally equivalent reflexive attentional orienting effects.

GENERAL DISCUSSION

The present study was conducted to test the hypothesis that humans may have evolved neural mechanisms specialized for orienting attention to biologically based social cues. To answer this question, we used fMRI to test whether different regions of the brain were engaged when orienting to biologically based eye gaze cues and nonbiologically based arrow cues. Experiment 1 revealed an extensive and highly similar BOLD response for both types of cue, suggesting that, at least in the context of the present study, the same cortical network subserved attentional orienting to social and nonsocial cues. Although we did not identify distinct neural modules that responded only to eye gaze cues, there were specific regions that responded more vigorously to eye gaze relative to arrow cues, including the lateral occipital cortex. The results of Experiment 2, a follow-up ERP study, revealed that this larger BOLD response in the occipital cortex may well have been attributable to the eye gaze cues evoking a larger sensory gain effect for targets presented at attended locations.

Before discussing the broader implications of the present study, it is important to note that the present results contrast that of a previous fMRI study that reported that orienting to arrows recruited areas of the frontal and parietal attention network, but gaze cues did not (Hietanen et al., 2006). Hietanen et al. (2006) reported the non-overlapping networks for directional arrow and diverted gaze cues within the context of a blocked fMRI design that required an initial subtraction of activity observed in

a baseline control conditions that consisted of a nondirectional line stimulus and an undiverted gaze stimulus, respectively. Given the blocked design of the Hietanen et al., it is possible that either the target stimuli and/or the undiverted gaze stimulus in the control condition evoked activity in the frontal and parietal cortex, thus reducing the likelihood of revealing activations in those areas in the diverted gaze condition (the authors themselves note this possibility on p. 411). In contrast, the present event-related design permitted the deconvolution of activity evoked by gaze cues which were physically identical to the arrow cues without relying on nonequivalent baseline control conditions, thereby making the present design much more sensitive to detecting activity in the frontal and parietal cortex evoked by gaze cues.

A Cortical Network for Reflexive Attention to Meaningful Stimuli

In addition to our primary research goal—the question of whether there are distinct neural systems for attentional orienting to social and nonsocial cues—the present study addresses more generally the neural systems involved in reflexive attentional orienting to centrally presented cues. There has been some debate as to whether reflexive and volitional orienting are underlain by distinct neural mechanisms. Early work by Posner (1980), as well as more recent studies (Sapir, Soroker, Berger, & Henik, 1999) provided evidence of a role for the superior colliculus in reflexive attentional orienting. This role for the superior colliculus, however, is largely associated with abrupt peripheral events that activate the eye movement system (Rafal & Smith, 1990; Rafal, Calabresi, Brennan, & Sciolto, 1989). As the present study used centrally presented cues, and prohibited eye movements, it is not surprising that there was no BOLD activation found for the superior colliculus.

To date, there have been very few neuroimaging studies of reflexive attention in and of itself. The few that have been conducted have manipulated orienting via abrupt peripheral events. These results are difficult to compare with the vast majority of neuroimaging studies of attention, which typically use centrally presented predictive arrow cues to induce volitional attentional shifts (cf. Ristic & Kingstone, 2006 for a detailed consideration of this issue). By using a nonpredictive centrally presented directional cue in the present study, the results can be directly compared to the existing literature regarding the cortical networks associated with volitional attention without confounding reflexive attention with eye movement preparation.

The large fronto-parietal networks that showed a significant BOLD response when orienting to both eye and arrow cues map very well onto the dorsal and ventral fronto-parietal networks identified by Corbetta and Shulman (2002). Their meta-analysis revealed that the dorsal fronto-parietal network, consisting of regions of

the superior parietal lobule, intraparietal sulcus, middle and superior frontal gyri, has been, in most studies, associated with volitional or willful processes for directing spatial attention. The ventral fronto-parietal network, conversely, consisting of regions in the temporal–parietal junction (inferior parietal lobule and STG), as well as the ventral frontal cortex, has been associated with reflexive orienting to particularly salient stimuli or infrequent events. This pattern of results seems to support the idea that, indeed, distinct neural systems underlie volitional and reflexive attentional orienting. However, it is grounded largely on a confound of central and peripheral cueing.

The present results demonstrate that when this confound is removed, both dorsal and ventral fronto-parietal networks are involved in reflexive orienting to a directional cue presented at fixation. This finding suggests an interaction between dorsal and ventral fronto-parietal networks in reflexive attentional orienting to meaningful stimuli. This is consistent with Corbetta and Shulman's (2002) alternative proposal that effective reflexive attentional orienting to a spatial location may require the co-activation of both these networks—the ventral network subserving a circuit-breaking or attentional reorienting function in response to a salient or meaningful stimulus, and the dorsal network contributing a spatial selectivity function. An additional implication of the present results is that dorsal and ventral fronto-parietal networks should not simply be functionally mapped to volitional (endogenous) and reflexive (exogenous) orienting processes. Nor for that matter should central and peripheral cueing be mapped to volitional and reflexive orienting, as is mistakenly done on occasion (Vecera & Rizzo, 2006).

Biologically Relevant Cues as Inherently Meaningful Stimuli

A direct comparison of the cortical networks associated with attentional orienting to eye gaze and arrow cues revealed two clusters in the frontal cortex (in addition to those found in the lateral occipital cortex) that were more vigorously engaged by eye gaze than by arrow cues. Although these regions showed a BOLD response for both eye gaze and arrow cues, eye gaze cues evoked a significantly larger BOLD response in these areas. This finding is consistent with previous work suggesting that eye gaze cues do not engage distinct neural mechanisms for orienting attention, but recruit the same neural resources more efficiently (Quadflieg et al., 2004). Both of the ventral frontal regions showing a larger BOLD response for eye gaze cues are part of the ventral fronto-parietal network, which is associated with attentional reorienting to particularly salient or meaningful stimuli. Enhanced BOLD activity in these ventral frontal regions is consistent with the idea that eye gaze cues are particularly meaningful and are recognized by the attentional system as such.

This result lends itself to the provocative possibility that other types of inherently meaningful stimuli may also induce reflexive attentional orienting, and bring about enhanced activity in these ventral frontal regions. Our results indicate that eye gaze is one such meaningful cue. Other biologically relevant social stimuli, such as finger pointing or head turning, may also serve as particularly effective cues for ventral fronto-parietal activation and reflexive orienting. In addition, nonsocial stimuli that are inherently meaningful in their provision of information directly useful for planning and coordinating adaptive behavior, such as looming stimuli (Franconeri & Simons, 2003), or one's heading point or obstacles on one's path during self-motion, may serve as particularly effective reflexive cues.

Critical Considerations

Does the STS Specialize in Biological Relevance?

Interestingly, the STS, a structure implicated in attentional orienting to eye gaze stimuli in both lesion (Akiyama et al., 2006) and fMRI (Hoffman & Haxby, 2000) studies, did not show greater activation for eye gaze than for arrow cues. Akiyama et al. (2006) showed that a patient with a circumscribed lesion to the right STG was not able to orient attention to eye gaze stimuli, but orienting to arrow cues was left intact. The authors concluded that the STS specializes in processing eye gaze.

Although this result may seem to provide compelling evidence for the specialization of the STS for processing eye gaze, it is important to note that the eye gaze and arrow cues employed in the Akiyama study consisted of physically different stimuli. Thus, it is quite possible that the physical construction of the stimuli, rather than the meaning of the stimuli, produced the observed differences in orienting. In any case, it is also true that although Akiyama et al.'s results speak to the necessity of the STS in processing eye gaze, they do not preclude the engagement of the STS during orienting to arrow cues if the STS is functionally intact. Our data show that when cue-type and stimulus-construction are not confounded and the STS is functionally intact, there is a significant BOLD response in the right STS for both eye gaze and the arrow cue conditions (Figure 2).

Are the Present Orienting Effects Truly Reflexive?

One might question whether reflexive orienting to gaze and arrows cues should be considered spatially reflexive, for instance, in light of the fact that volitional top–down processes are critical to whether the stimulus cue is perceived as an eye or an arrow. This concern, however, confuses volitional acquisition of a percept with volitional spatial orienting itself. In all cases, and regardless of whether an eye or arrow percept is acquired,

participants have no incentive to attend volitionally to the cued location, that is, they are informed repeatedly that the direction of the cue never predicts reliably the location of a target. Nevertheless, and for both percepts, attention is shifted rapidly and consistently to the cued location, thereby satisfying the key criteria for reflexive spatial orienting (Ristic, Wright, & Kingstone, 2007; Gibson & Kingstone, 2006; Ristic et al., 2002; Tipples, 2002; Friesen & Kingstone, 1998). With this point in place, it is also important to note that although both cues engage reflexive orienting, and their behavioral effects in the present study are equivalent, it does not follow that their attention effects must be identical on all fronts (Ristic, Wright, & Kingstone, 2007). Indeed, as we found in the present study, the sensory gain effect from eye gaze cues is significantly greater than for arrow cues.

Conclusion

The present study demonstrates that reflexive social attention, at least in the context of perceiving eye gaze cues, does not require the involvement of a specialized attentional module network per se. Rather, eye gaze cues more vigorously engage ventral frontal regions within a common attentional network and bring about a larger sensory gain effect at the attended location than do arrow cues. Ventral frontal regions associated with the detection of stimulus salience were more highly activated by eye gaze than arrow cues, even though these cues consisted of identical physical stimulation on the retina. Thus, the salience of eye gaze cues cannot be attributed solely to low-level visual properties such as high contrast or spatial frequency. Rather, any benefit for eye gaze cues had to have been brought about by how that cue was being represented. In other words, the enhanced sensory processing at the gazed-at location occurred because the eye gaze cue was more salient to the attentional system, presumably because eyes are socially and biologically meaningful (Birmingham, Bischof, & Kingstone, in press-a, in press-b). A final, intriguing implication of these data, is that our ability to orient volitionally and reflexively to socially irrelevant stimuli, including arrowheads, may have arisen as a useful by-product of a system that developed first, and foremost, to promote social orienting to stimuli that are biologically relevant.

Acknowledgments

This work was supported by graduate student awards to C. T. by NSERC and MSFHR; grants to T. H. by NIH, NSERC, and MSFHR; and grants to A. K. by NSERC and MSFHR. We thank the comments by Todd Heatherton and two anonymous reviewers on a previous version of this manuscript.

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