

Automatic attention orienting by social and symbolic cues activates different neural networks: An fMRI study

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Visual attention can be automatically re-oriented by another person's non-predictive gaze as well as by symbolic arrow cues. We investigated whether the shifts of attention triggered by biologically relevant gaze cues and biologically non-relevant arrow cues rely on the same neural systems by comparing the effects of gaze-cued and arrow-cued orienting on blood oxygenation level-dependent (BOLD) signal in humans. Participants detected laterally presented reaction signals preceded by centrally presented non-predictive gaze and arrow cues. Directional gaze cues and arrow cues were presented in separate blocks. Furthermore, two separate control blocks were run in which non-directional cues (straight gaze or segment of a line) were used. The BOLD signals during the control blocks were subtracted from those during the respective blocks with directional cues. Behavioral data showed that, for both cue types, reaction times were shorter on congruent than incongruent trials. Imaging data revealed three foci of activation for gaze-cued orienting: in the left inferior occipital gyrus and right medial and inferior occipital gyri. For arrow-cued orienting, a much more extensive network was activated. There were large postcentral activations bilaterally including areas in the medial/inferior occipital gyri and medial temporal gyri and in the left intraparietal area. Interestingly, arrow cuing also activated the right frontal eye field and supplementary eye field. The results suggest that attention orienting by gaze cues and attention orienting by arrow cues are not supported by the same cortical network and that attention orienting by symbolic arrow cues relies on mechanisms associated with voluntary shifts of attention.

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Introduction

Seeing another person with gaze directed away from oneself can trigger a shift of visual attention in the cued (gazed at) direction (e.g., Driver et al., 1999; Friesen and Kingstone, 1998; Friesen et al., 2005; Hietanen, 1999, 2002; Langton and Bruce, 1999). One of the most interesting findings related to this gaze-triggered attention orienting is that it seems to be automatic or reflexive. Namely, in studies employing the spatial cuing paradigm (Posner, 1980), reaction times to laterally presented targets were influenced by non-predictive gaze cues (i.e., the probability of valid and invalid cuing was equal) presented with relatively short time delays (even less than 100 ms, Hietanen and Leppänen, 2003, Experiment 4) between the cue and target onsets.

Before the first study reporting of these findings (Friesen and Kingstone, 1998), the common view on the field was that automatic or reflexive re-orienting of visual attention can be triggered by abrupt visual onsets occurring in the visual periphery but not by centrally presented symbolic stimuli (Jonides, 1981; Posner, 1980). As gaze-cued attention shifts seemed to fulfil the criteria of automatic attention orienting, it was postulated that this occurs because another individual's face with an averted gaze is a special type of a socially and biologically relevant stimulus (Friesen and Kingstone, 1998). However, shortly after the first studies describing gaze-cued attention orienting, a number of other studies indicated that non-predictive arrow cues presented at short cue–target intervals also triggered shifts of visual attention in automatic fashion (Hommel et al., 2001, Experiment 3a; Ristic et al., 2002; Tipples, 2002).

Now, these results raise a very important question. If visual attention is automatically shifted also by centrally presented, biologically non-relevant, symbolic cues such as arrows, what evidence do we have to support the notions that attention orienting by gaze is special and possibly mediated by dedicated neural mechanisms? One line of evidence comes from studies showing that the gaze cuing is dependent not only on the low-level

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geometric information but also on the usual contrast polarity between the dark iris/pupil and the light sclera. Reversing the contrast polarity reverses the direction of the cuing effect (Tipples, 2005). Since the first studies reporting automatic attention orienting by arrow cues, there have also been a few studies directly comparing attention orienting by gaze and arrow cues. Ristic et al. (2002) measured behavioral reaction times to detection of targets preceded by non-predictive gaze and arrow cues and showed that the cuing effects by gaze and arrow cues were indistinguishable. However, more recently, Friesen et al. (2004) provided new evidence that, even though both gaze and arrow cues seem to be capable of eliciting automatic shifts of attention, gaze cuing, nevertheless, seems to be “more reflexive”. Friesen et al. (2004) manipulated the participants’ subjective expectancy and showed that, despite of a strong subjective bias to expect the target to appear at the opposite to gazed-at location, the gaze cues, nevertheless, resulted in attention shifts to the gazed-at locations. Similar results were reported earlier by Driver et al. (1999, Experiment 3). Importantly, however, Friesen et al. (2004) showed that this kind of counter-predictive cuing was not observed with arrow cues. Moreover, studies with brain-lesioned patients have also suggested that reflexive shifts of attention triggered by gaze and arrow cues may not rely on similar mechanisms (Kingstone et al., 2000; Ristic et al., 2002; Experiment 3; Vuilleumier, 2002).

Kingstone et al. (2004) investigated brain activation during an attention orienting task by using an ambiguous figure that could be perceived as a gaze cue (a hat pulled down to the eyes) or as a nonsocial directional cue (a car with eccentric wheels). The standard behavioral cuing effect was observed in both instances. When contrasting orienting by (perceived) gaze and car cues, the results revealed only one locus of activation. Activity in the area of superior temporal sulcus (STS, an area known to be involved in face and gaze processing, see e.g., Akiyama et al., 2006; Allison et al., 2000; George et al., 2001; Hoffman and Haxby, 2000; Pelphrey et al., 2004) was increased when the stimulus was perceived as eyes as compared to condition in which it was perceived as a car. In addition, Hooker et al. (2003) have shown that STS is more strongly activated when participants judge whether the eyes shift to one of the pre-determined target locations than when they perform a comparable task with arrows. These results provide strong evidence that visual attention orienting by gaze cues really relies on visual information from the face analyzed by gaze-specific mechanisms and not by some kind of an all-around mechanism analyzing all types of visual directional information (i.e., also symbolic cues).

As this study is targeted to investigate the possible differences in the neural systems supporting gaze-cued and arrow-cued attention orienting and as one possible difference between these two types of cuing may be related to differences in the role of top-down control processes in gaze vs. arrow triggered cuing (cf. Friesen et al., 2004), it is useful to contemplate the present study against those which have compared the neural substrates behind endogenous and exogenous attention orienting. Endogenous orienting refers to voluntary shifts of attention and, as described above, it is commonly investigated by using centrally presented arrow cues that predict the target location with a high probability (e.g., 70–80%). Exogenous orienting, in turn, refers to stimulus-driven, automatic orienting, and it is usually studied by cuing the targets with peripheral illumination changes which do not predict the target location.

The cognitive and neural mechanisms supporting endogenous and exogenous orienting of visual attention have been intensively

investigated since the early characterization of these two modes of attention orienting. In a recent review, Corbetta and Shulman (2002) summarized the findings from functional imaging studies and suggested that visual attention is controlled by two partially segregated neural systems: voluntary control of visuospatial attention is associated with activation in the dorsal parietal and superior frontal cortices (a dorsal frontoparietal network), whereas reflexive control of attention involves neural systems in the temporoparietal and inferior frontal cortices (a ventral frontoparietal network). Interestingly, a recent meta-analysis of 59 brain imaging studies demonstrated that the networks responsible for gaze perception are more similar to those involved in reflexive than to those involved in voluntary shifts of attention and eye movements (Grosbras et al., 2005). The analysis indicated that gaze perception, reflexive shifts of covert attention, and visually guided eye movements activate the temporoparietal junction (TPJ) in proximity of the ascending branch of the superior temporal sulcus (STS) in the right hemisphere. Grosbras et al. proposed that this area together with a frontoparietal network forms a system which is involved in overt and covert attention orienting triggered by peripheral as well as by gaze cues.

In the present study, we aimed to directly characterize the neural mechanisms involved in automatic shifts of attention triggered by gaze cues and arrow cues. Especially, we aimed at finding and comparing neural activity related to the processing stages other than (i.e., following) those involved in the visual analysis of the directional cues themselves. It is entirely possible that even though the visual analysis of gaze and arrow cues were carried out by different neural systems – which, indeed, appears likely (cf. Kingstone et al., 2004) – the subsequent orienting of attention could be based on workings of the same brain mechanisms. To this end, we measured brain activity with functional magnetic resonance imaging (fMRI) while the participants were performing standard cuing tasks with gaze and arrow cues. With both types of cues, the participants performed the cuing task in two different conditions: in a condition involving cue-triggered shifts of attention (congruent and incongruent trials) and in a condition without cue-triggered attention shifts (neutral trials: a straight gaze or a segment of a line). By subtracting the blood oxygenation level-dependent (BOLD) signal during the condition without cue-triggered attention shifts from that involving cue-triggered shifts of attention, and by doing this separately for data collected during gaze-cued and arrow-cued orienting, we aimed at comparing whether the *attention orienting* by gaze and arrow cues is subserved by the same or different neural mechanisms.

We also present tentative hypotheses regarding the expected differences. Based on the earlier findings suggesting that gaze-cued orienting may be more reflexive than arrow-cued orienting (Friesen et al., 2004), we expect to find that gaze cuing involves activation of the network implied in involuntary control of attention, whereas arrow cuing involves activation in the systems associated with voluntary orienting. It is important to note that the neural networks activated by gaze and arrow cues should not be expected to be exactly identical with those postulated in the ventral and dorsal frontoparietal networks (Corbetta and Shulman, 2002) because the characterization of these networks was largely based on studies using non-predictive peripheral abrupt onset cues and predictive central arrow cues, respectively. Nevertheless, we expect that, if we find differences in the networks activated by gaze and arrow cues, the networks will resemble those involved in involuntary and voluntary orienting, respectively.

Methods

The study protocol was reviewed and approved by the ethical committee of Turku University Hospital, and all participants signed ethical committee-approved, informed consent forms. The study was performed in accordance with the Declaration of Helsinki.

Participants

We scanned 10 neurologically intact, volunteer men with a mean age of 26 years. All participants had normal or corrected-to-normal vision (self-reported) and those who were using vision correction used contact lenses during the scanning.

Apparatus

Functional and anatomical volumes were collected with Philips Gyroscan Intera 1.5 T CV Nova Dual scanner. High-resolution anatomical images (1 mm³ resolution) were acquired using a T1-weighted sequence (TR 25 ms, TE 4.6 ms, flip angle 30°, scan time 375 s). Whole-brain functional volumes were acquired using a gradient echo pulse sequence (TR=3000 ms, TE=50 ms, 90° flip angle, 192 mm FOV, 64*44 matrix, 62.5 kHz bandwidth, 4.0 mm slice thickness, 0.5 mm gap between slices, 30 interleaved slices with bottom to top slice ordering), sensitive to blood oxygen level-dependent (BOLD) contrast. The stimulus presentation and behavioral data collection were controlled with Presentation computer program (Neurobehavioral Systems, Inc.). Stimuli were projected from an LCD projector onto a non-magnetic screen mounted at the foot of the bore, and an angled mirror reflected images on the screen to the participants' field of vision. The participants' eye movements were not controlled for.

Experimental stimulus displays

The initial display (see Fig. 1) consisted of a fixation cross (diameter 0.5°) centered on the screen. The face displays (gazing to left, right, or straight ahead) consisted of black line drawings of a round schematic face subtending 7° and centered on the middle of the screen. The eyes subtended 1.5°, were located on the central horizontal axis, and were 2° apart across the central vertical axis. Black-filled circles inside the eyes represented pupils. The pupils subtended 0.7°, were centered vertically to the eyes, and were just touching left or right side of the eye or were centered (neutral trials) in the eyes. The arrow displays (an arrow pointing to left or right, or a segment of a line) consisted of a circle subtending 7° centered on the screen, a horizontal line subtending 5° centered on the central vertical axis, and the arrow tips at the beginning and at the end of the horizontal line. The arrow tips pointed to the left, right, or were vertical bars (neutral trials). The target stimulus demanding response was a black asterisk (diameter 0.5°) presented 2° to the left or right of the perimeter of the cue displays.

Procedure

Participants were scanned individually in single sessions, and testing time totaled approximately 1 h per participant including acquisition of the T1-weighted images. Upon arriving to the laboratory, participants gave a written informed consent and completed a checklist for MRI exclusion factors. The purpose of the study was explained to the participants. In instruction, the cues

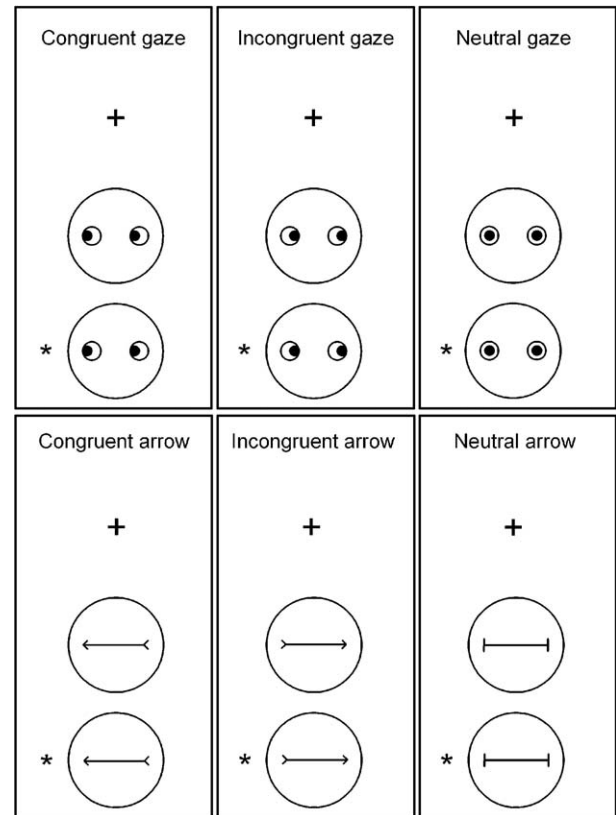


Fig. 1. Examples of congruent, incongruent, and neutral trials with gaze and arrow cues. Each trial consisted of the appearance of the fixation cross followed by the cue and laterally presented target asterisk.

were introduced as faces and traffic signs with arrows. It was emphasized that the gaze or arrow direction did not predict the side on which the reaction signal would appear. Next, the participants were presented with twenty practice trials on a laptop computer. Finally, the participants were placed in the scanner, a response box was given to them, and they were told how to respond in the trials with the response button.

The presentation of the experimental trials was time-locked with the acquisition of the functional images, each trial beginning simultaneously with the whole-brain functional volume scan. One experimental trial (see Fig. 1) lasted for 3000 ms and consisted of the following events: a fixation cross appeared at the center of the screen for 500 ms. Next, the cue stimulus appeared on the screen, and after 200 ms period of cue presentation, the reaction signal was presented either at the left or right to the cue stimulus (except for catch trials). Thus, the stimulus-onset-asynchrony (SOA) between the cue and target was 200 ms. Participants responded by pressing a single response key after detecting the target. Both the cue and the target remained visible until the end of the trial period.

Each participant performed 40 blocks of the task. There were four types of blocks: one containing congruent and incongruent gaze cue trials, one containing neutral gaze cue trials, one containing congruent and incongruent arrow cue trials, and one containing neutral arrow cue trials. Each block consisted of ten trials. In the blocks which contained congruent and incongruent trials, four of the trials were congruent and four incongruent. In all blocks, two of the trials were catch trials (i.e., no reaction signal was presented). Altogether, each participant performed ten blocks

of each type, totaling 100 trials of each type and a grand total of 400 trials. The different types of blocks were presented in a loop (repeated ten times) in which the blocks were in the following order: neutral arrow, arrow cuing, neutral gaze, and gaze cuing. There was a short break (approximately 30 s) after every eight blocks. After the experiment, participants were interviewed about complications experienced while being scanned and debriefed about the purposes of the experiment.

fMRI data analysis

SPM2 software was used for the data analysis (Friston et al., 1994). First, functional images were motion corrected and unwarped. Next, the anatomical volume was spatially normalized using a template from the MNI series (Montreal Neurological Institute, Quebec, Canada; Evans et al., 1993), and these normalization parameters were subsequently applied to the functional images. A 3 mm Gaussian kernel was used for spatial smoothing of the images. Finally, 128 Hz high-pass filter was applied. Statistical analysis was performed for the overall group of subjects using the general linear model. To reveal areas uniquely activated by orienting of attention by gaze and arrow cues, one-way *t*-contrasts were computed separately for the gaze and arrow conditions with their respective control conditions. Moreover, to reveal areas activated more strongly by arrow cuing than gaze cuing, the aforementioned activation maps were also contrasted with each other. A minimum cluster size of 20 voxels and FWE-corrected alpha level of 0.05 was used for statistical testing.

Results

Reaction time data

On average, participants made 0.6% catch trial errors (pressed the response button when there was no reaction signal). Reaction time data from correct responses were collapsed across the blocks, and anticipations (reaction times <80 ms) and retardations (reaction times 2 standard deviations above individual mean) were excluded from the data analysis. These accounted for 1.3% of the trials. Next, the mean RT in each cuing condition was calculated for each participant. These results are presented in Fig. 2.

In order to analyze whether the laterally oriented gaze and arrow cues shifted the participants' attention, RTs in congruent and

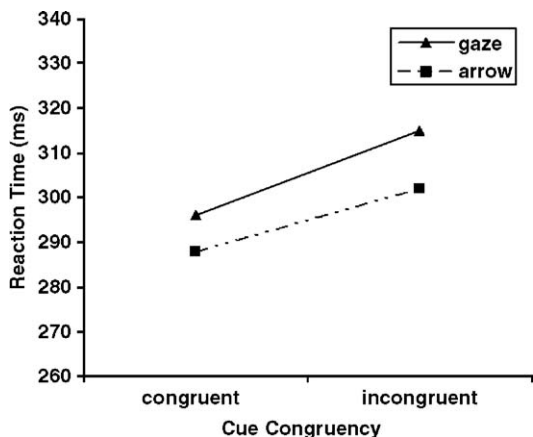


Fig. 2. Mean reaction times as a function of cue congruency and cue type.

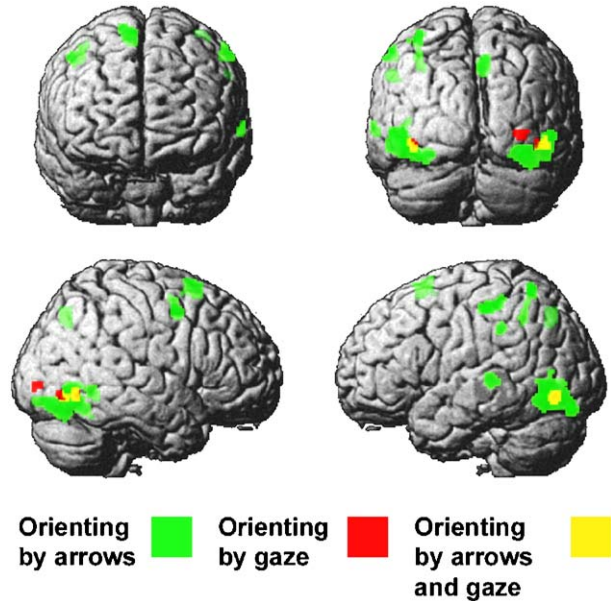


Fig. 3. Regions of brain showing greater BOLD responses to directional versus non-directional arrow cuing (green and yellow) and to directional versus non-directional gaze cuing (red and yellow).

incongruent conditions cued by gaze and arrow cues were compared by subjecting them to a 2 (Cue congruency: congruent/incongruent) × 2 (Cue type: arrow/gaze) repeated measures ANOVA. The analysis yielded significant main effects for congruency ($F_{1,9}=25.0, P<0.001, \eta_p^2=0.74$) and cue type ($F_{1,9}=16.3, P<0.01, \eta_p^2=0.65$). Thus, the reaction times were shorter after congruent (292 ms) than incongruent (309 ms) cues as well as after the arrow (295 ms) than gaze (305 ms) cues. Furthermore, the congruency × cue type interaction was significant ($F_{1,9}=7.2, P<0.03, \eta_p^2=0.44$). Because of the significant interaction, the effect of cuing by both cue types was confirmed with paired comparisons. These analyses showed that the reaction times were shorter in congruent than incongruent trials in both the gaze cuing (296 vs. 315 ms, $t_9=6.1, P<0.001$) and arrow cuing conditions (287 vs. 302 ms, $t_9=3.8, P<0.01$). The significant interaction resulted from the cuing effect ($RT_{\text{incongruent}}-RT_{\text{congruent}}$) being slightly stronger for the gaze (19.2 ms) than arrow (14.1 ms) cues ($t_9=2.7, P<0.03$). Reaction times in the non-directional gaze and arrow blocks were also analyzed. These analyses showed that the mean RT was the same, 300 ms, in both blocks.

Imaging data

Fig. 3 shows statistical maps of the regions in which the BOLD response was greater during the directional cuing (congruent and incongruent trials) than non-directional cuing (neutral trials). In the maps, the green color indicates regions uniquely activated by arrow cuing, the red color indicates regions uniquely activated by gaze cuing, and the yellow color indicates regions activated by both arrow cuing and gaze cuing. Coordinates, *T* values, and cluster sizes of regions showing greater response during directional than non-directional gaze and arrow cuing are presented in Table 1. The results showed that a wider network of cortical areas was activated during arrow-cued than gaze-cued shifts of visual attention. Attention orienting by gaze cues increased activation in three

Table 1

Brain regions showing greater BOLD response to directional than non-directional cuing by gaze (upper) and arrow (lower) cues

Region	Laterality	BA	x	y	z	T	K
<i>Gaze cuing</i>							
IOG	L	19	-40	-74	-8	5.67	25
MOG, IOG	R	19/37	48	-64	-8	5.56	31
MOG	R	18	30	-90	0	5.46	24
<i>Arrow cuing</i>							
MOG, IOG	L	18/19/37	-48	-68	-10	6.90	407
MOG, ITG	R	37	48	-66	-12	7.05	219
MOG, FG, IOG	R	18/19	34	-82	-14	6.48	226
MTG	L	22/21	-64	-30	2	6.27	37
MTG	R	37	48	-54	-6	5.83	40
Precuneus	R	7	8	-70	44	6.32	71
IPL	L	40/7	-36	-58	62	5.89	75
IPL	L	40	-52	-38	36	5.82	28
PG	L	2/40	-56	-28	50	5.84	83
MFG (FEF)	R	6	46	2	48	5.77	63
SFG (SEF)	R	6	8	12	64	6.69	111

Note. Coordinates reflect positions relative to MNI atlas (Montreal Neurological Institute, Quebec, Canada; Evans et al., 1993). BA=Brodmann area, K=number of voxels belonging to cluster, FEF=frontal eye field, FG=fusiform gyrus, IOG=inferior occipital gyrus, IPL=inferior parietal lobule, ITG=inferior temporal gyrus, MFG=middle frontal gyrus, MOG=middle occipital gyrus, PG=postcentral gyrus, SEF=supplementary eye field, SFG=superior frontal gyrus.

posterior clusters, one in left hemisphere and two in right hemisphere. In left hemisphere, the activated area was located in inferior occipital gyrus (IOG). In right hemisphere, one focus of activation was located in medial/inferior occipital gyri (MOG/IOG) and another more posteriorly and more medially in right medial occipital gyrus (MOG). Notably, orienting of attention by gaze did not increase activation in the frontal areas.

Orienting of attention by arrows increased activation in several posterior clusters in both hemispheres. On the ventral surface of the left hemisphere, the arrow cues activated similar areas than did the

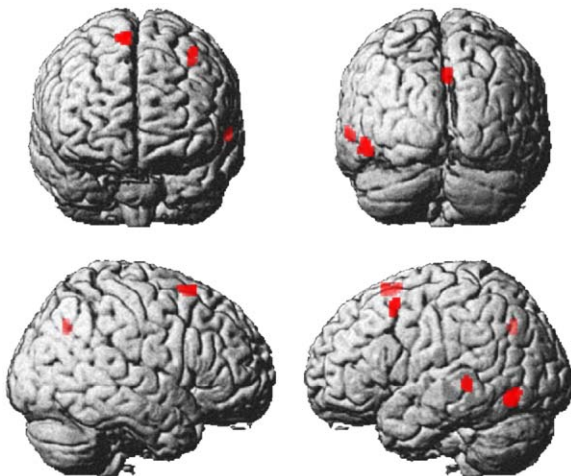


Fig. 4. Regions of brain showing greater BOLD responses to attention orienting by arrow cues (directional versus non-directional arrow cuing) than to attention orienting by gaze cues (directional versus non-directional gaze cuing).

Table 2

Brain regions showing greater response to arrow cuing than to gaze cuing (upper) and to non-directional gaze than to non-directional arrow cues (lower)

Region	Laterality	BA	x	y	z	T	K
<i>Arrow cuing–Gaze cuing</i>							
MOG, ITG	L	37/19	-48	-66	-10	6.32	56
Precuneus	R	7	4	-66	38	5.65	28
MTG	L	22/21	-60	-36	0	5.51	23
MFG (FEF), SFG (SEF)	L	6/8	-36	12	54	5.61	31
SFG (SEF)	R	6	10	12	62	6.04	59
<i>Non-directional gaze–Non-directional arrow</i>							
FG, MOG	L	19/18	-32	-82	-18	5.60	28
FG	R	19/37	40	-60	-20	5.31	30

Note. Coordinates reflect positions relative to MNI atlas (Montreal Neurological Institute, Quebec, Canada; Evans et al. 1993). BA=Brodmann area, K=number of voxels belonging to cluster, FEF=frontal eye field, FG=fusiform gyrus, ITG=inferior temporal gyrus, MFG=middle frontal gyrus, MOG=middle occipital gyrus, MTG=middle temporal gyrus, SEF=supplementary eye field, SFG=superior frontal gyrus.

gaze cues, but they were more extensive comprising not only IOG but also MOG cortex. Also on the ventral surface of the right hemisphere, similar to gaze cuing, there were two clusters of activated areas which, however, were again much more extensive than those activated by gaze cues. These clusters comprised areas in IOG, MOG, FG (fusiform gyrus), and ITG (inferior temporal gyrus). In addition, orienting of attention by arrows uniquely increased activation in left and right middle temporal gyrus (MTG), right precuneus, in two clusters in left inferior parietal lobule (IPL), and in a cluster located in left postcentral gyrus (PG). Most interestingly, arrow-cued orienting increased activation also in two frontal clusters: in right frontal eye field (FEF) and supplementary eye field (SEF).

In order to analyze the regions where the arrow cuing (directional arrow–non-directional arrow) resulted in statistically stronger activation than the gaze cuing (directional gaze–non-directional gaze), we contrasted these two activation maps. Fig. 4 depicts the brain regions showing greater BOLD responses to attention orienting by arrow cues than to attention orienting by gaze cues. Coordinates, T values, and cluster sizes of these regions are presented in Table 2 (upper part). Three posterior clusters were more strongly activated by arrow cuing than by gaze cuing. These were located in left middle occipital/inferior occipital gyri (MOG/IOG), in left middle temporal gyrus (MTG), and in right precuneus. Arrow cuing elicited stronger activation than gaze cuing also in two frontal clusters: in left frontal eye field/supplementary eye field (FEF/SEF) and in right supplementary eye field (SEF).

Finally, we wanted to assess whether the schematic face stimuli activated the brain regions known to be associated with face processing. To this purpose, we contrasted non-directional gaze and non-directional arrow conditions. This analysis showed only two activation clusters which located in fusiform/middle occipital gyri (FG/MOG) in both hemispheres (Table 2, lower part).

Discussion

Our main finding was that, although the behavioral data showed that both non-predictive gaze cues and non-predictive arrow cues resulted in a typical RT facilitation for congruent vs. incongruent

cuing conditions in a spatial orienting task, the imaging data suggested that attention orienting by gaze cues and attention orienting by arrow cues are supported by partially segregated cortical networks. Two types of analyses were performed on the imaging data. First, the analysis was based on subtraction of BOLD signals elicited by non-directional gaze cues (straight gaze) and non-directional arrow cues (a segment of a line) from the signals elicited by respective directional cues (laterally averted gaze and pointing arrows) and, consequently, on comparison of parametric maps resulting from these subtractions. These subtractions were performed in order to find differences in brain activity evoked by gaze-cued and arrow-cued attention orienting independent of processes related to visual perception of these spatial cues. Second, we also contrasted these two parametric maps in order to analyze the regions which exhibited stronger brain activity to arrow cuing than to gaze cuing.

In the present study, the gaze and arrow cues were simple schematic drawings of faces and “traffic signs” and did not differ widely in their low-level visual features. Therefore, the comparison of the neural networks supporting attentional shifts triggered by these two types of schematic cues is not confounded by such factors which often complicate the comparison of networks supporting exogenous and endogenous orienting triggered by peripheral illumination changes and centrally presented symbolic cues, respectively (for discussion and taking these problems into consideration, see Kincade et al., 2005). Furthermore, in the present study, both gaze-cued and arrow-cued tasks contained an equal number of congruent and incongruent trials, unlike in studies comparing non-predictive peripheral cuing and predictive symbolic cuing. This feature of the design also makes the comparison between the cue types more straightforward.

The results showed that the networks activated by gaze cues and arrow cues were partly overlapping in the posterior occipito-temporal areas. However, the activated areas by arrow cues were much larger than those activated by gaze cues. Moreover, the attention orienting by arrows uniquely activated areas in the parietal and frontal cortices. In the Introduction section, we presented hypotheses regarding the expected differences between areas activated by gaze cuing and arrow cuing. We expected that gaze cuing would activate a network which would resemble that suggested to be involved in involuntary control of attention, whereas arrow cuing was expected to activate a network which would share similarities with that suggested to be involved in voluntary orienting. Generally, the present findings seemed to support our hypotheses. One important finding supporting these hypotheses was that the spatial extent of activated areas was smaller for gaze-cued than arrow-cued orienting, a finding consistent with a view that gaze-cued orienting is more reflexive than arrow-cued orienting (cf. Kim et al., 1999; Nobre et al., 1997; Rosen et al., 1999).

Gaze cuing increased activation in three posterior areas: left IOG, right MOG/IOG, and a more posterior right MOG. The increased activation in these extrastriate areas is likely to reflect the enhanced visual processing due to attention (cf. Brefczynski and DeYoe, 1999; Hopfinger et al., 2000; Kastner et al., 1998; Martinez et al., 2001; Yantis et al., 2002). Notably, after the subtraction, there was no increased activation in the STS/STG and FFA regions implicated for gaze and face processing (Haxby et al., 2000). This shows that our experimental design worked as intended. By subtracting the activity evoked by non-directional gaze and arrow cues from the activity evoked by directional gaze and arrow cues,

we intended to abolish the activation elicited by visual processing of the cues *per se*. Instead, the contrast between non-directional gaze cue (face) and non-directional arrow cue (traffic sign) revealed activation in the area of fusiform/middle occipital gyri. This provides evidence for our schematic face stimulus activating the neural systems involved in face processing. In an fMRI study by Kingstone et al. (2004) in which they used an ambiguous figure (that could be perceived as eyes or a car) as a cue, the results showed greater activation in the STS area when the cue was perceived as eyes as compared to when it was perceived as a car. This pattern of results is likely to reflect the functional role of the STS in the visuo-perceptual analysis of gaze direction.

To somewhat of a surprise, the subtractions for gaze cue conditions did not reveal parietal activations, in other words, in the parietal areas, the activation was not stronger during directional gaze cuing than during non-directional straight gaze condition. Several earlier studies have shown increased activation in the superior and inferior parietal lobules (e.g., Kim et al., 1999; Rosen et al., 1999; Rushworth et al., 2001; Yantis et al., 2002) associated with the shifting of visual attention. However, recently Kincade et al. (2005) also reported results showing no increased activity in the intraparietal sulcus following exogenous cues. One possible explanation for the lack of parietal activation may be that the appearance of the lateral reaction signals acted, in fact, as a peripheral attention orienting cue. Thus, in the straight gaze condition, even though the gaze cue itself would not trigger shifts of visual attention, the lateral reaction signals did and activated the parietal mechanisms involved in reflexive orienting of attention. Consequently, it is possible that, if the parietal activation elicited by the directional gaze cues was not any greater than that evoked by the reaction signals, no parietal activation was observed after the subtractions.

Orienting by arrows increased activation in several clusters in both hemispheres. In the MOG/IOG cortex, the arrow cues activated similar areas to those activated by the gaze cues. As noted above, increased activation in these areas is likely to reflect enhanced visual processing due to allocation of attentional resources. Notably, the activation in these areas was more extensive for arrow than gaze cuing. In addition, orienting of attention by arrows uniquely increased activation in the left and right middle temporal gyrus (MTG). This finding is compatible with earlier results reporting stronger activation to voluntary than involuntary cuing in this area (Kim et al., 1999; Mayer et al., 2004; Rosen et al., 1999). The contrast analysis between the arrow and gaze cuing showed that in left MOG/ITG/MTG areas arrow cuing resulted in stronger brain activation than did gaze cuing. Attention orienting by arrows activated also left inferior parietal lobule (IPL). Earlier, Kim et al. (1999) and Rosen et al. (1999) have reported greater activity in this area during voluntary than involuntary orienting. The lateralization of the activation to the left parietal areas (IPL) by arrow cuing has been suggested to reflect increased verbal processing related to using symbolic cues (Mayer et al., 2004; Nobre et al., 1997). However, Mayer et al. (2004) have also reported stronger activation in the right IPL for voluntary than involuntary cuing. Arrow cuing also activated right precuneus, and similar findings related to voluntary control of attention have been reported earlier by several studies (Hopfinger et al., 2000; Kincade et al., 2005; Mayer et al., 2004).

One of the most interesting results of the present study was that orienting of attention by arrows increased activation in the right frontal eye fields (FEF) and supplementary eye fields (SEF), both

of which are parts of the cortical network involved in generation of visually guided saccades (for reviews, see [Dietrich and Brandt, 2000](#); [Grosbras et al., 2005](#)). Increased activation in these areas was not observed for gaze-cued orienting. The FEF, in addition to being related to programming and execution of overt eye movements (e.g., [Mesulam, 1981](#)), is commonly regarded to be a part of a neural network involved in voluntary shifts of covert attention ([Corbetta and Shulman, 2002](#), [Kastner and Ungerleider, 2000](#)). The FEF has been shown to activate during attention orienting by predictive arrow cues in several previous studies ([Corbetta et al., 2002](#); [Gitelman et al., 1999](#); [Hopfinger et al., 2000](#); [Mayer et al., 2004](#)). Thus, in addition to being activated by predictive symbolic cues, the present results show that FEF is also activated by non-predictive symbolic cues. The activation of the frontal eye fields during arrow-cued but not during gaze-cued orienting is very compatible with the suggestions that arrow-triggered shifts of attention are not as reflexive as those triggered by gaze direction cues ([Friesen et al., 2004](#)). The contrast analysis comparing the activation maps of arrow cuing and gaze cuing further supported this view by showing that arrow cuing resulted in stronger activation as compared to gaze cuing in clusters localizing in the areas of frontal eye fields/supplementary eye fields.

In contrast to the present results indicating no involvement of the frontal areas in gaze-cued attention shifts, [Vecera and Rizzo \(2006\)](#) recently reported results from a patient suffering from a frontal-lobe damage they tested in an attention orienting task with non-predictive gaze cues and peripheral cues. The results showed that the gaze cues were not effective in the shifting of visual attention in this patient, whereas peripheral cues resulted in a standard cuing effect. [Vecera and Rizzo](#) interpreted these results as suggesting that gaze cues direct attention in a voluntary (frontal-lobe dependent) and not in a reflexive manner. Although highly interesting, the lack of gaze cuing was observed with only one frontal-lobe damaged patient in that study. This, of course, warrants cautiousness in generalizing the results. For example, data from our own previous studies indicate that the gaze cuing effect is not exhibited by all healthy participants either. Therefore, attempts to try and reconcile the results by [Vecera and Rizzo \(2006\)](#) with the present ones may be futile, at the moment.

The behavioral results showed a cuing effect for both the gaze and arrow cues. Interestingly, the main effect of cue type indicated significantly shorter reaction times after the arrow than gaze cues. However, interaction between cue type of and cue congruency indicated that the cuing effect was stronger for the gaze than for arrow cues. [Ristic et al. \(2002\)](#) who also compared gaze cuing and arrow cuing found neither a significant effect of cue type nor an interaction between cue type and cue congruency. [Quadflieg et al. \(2004\)](#) investigated the effects of different types of cues (simple outline drawings) on visual orienting and reported (Experiment 3) shorter RTs when eyes were embedded in a glove than when arrows (within an oval frame) were embedded in a glove. [Quadflieg et al.](#) interpreted this result as suggesting that gaze cues may enhance the overall efficiency of attentional processing. It should be noted that, in the study by [Quadflieg et al.](#), the cues were dynamic (illusory motion), and it is possible that this feature may have contributed to the observed pattern of results.

However, there are also studies which have reported behavioral results similar to ours. [Vlamings et al. \(2005\)](#) who used dynamic gaze and arrow cues reported overall shorter reaction times after the arrow than gaze cues. Although not testing for their statistical

significance, [Friesen et al. \(2004\)](#) also reported numerically shorter RTs after arrow than gaze cues in their Experiments 2 and 1, respectively. Interestingly, [Friesen and colleagues](#) also employed non-directional cue trials (straight gaze or cross), and similar to ours, their results showed comparable RTs after non-directional social (gaze) and symbolic (arrow/cross) cues (see [Tables 1 and 2](#), in [Friesen et al., 2004](#)). At present, we cannot provide any explanation for the varying results between the present and earlier studies regarding the main effect of cue type. Importantly, however, we find it unlikely that this pattern of results could have explained the observed differences in the evoked brain activity. As described above, the differences in the evoked brain activity during gaze and arrow cuing seemed to have a resemblance with those observed during involuntary and voluntary cuing, and it is difficult to see how this pattern of results could have emerged if the activation results reflected some differences in the overall efficiency of gaze and arrow cues in engaging attentional processes.

In summary, the present neuroimaging study provided direct support for that automatic orienting of visual attention is supported by partially different mechanisms when shifts of attention are triggered by (non-predictive) gaze cues and when attention is shifted by arrow cues. Notably, in the present study, we characterized those neural processes involved in attention orienting which follow the initial perceptual coding of the cue (gaze or arrow) itself. Moreover, we also gained evidence that arrow-cued shifts of attention may be more dependent on the neural mechanisms suggested to be involved in voluntary shifts of attention. These results provide strong support for the notions that another person's gaze may, indeed, be a special stimulus in triggering reflexive shifts of visual attention.

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