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Right hemispheric dominance in gaze-triggered reflexive shift of attention in humans

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Abstract

Recent findings suggest a right hemispheric dominance in gaze-triggered shifts of attention. The aim of this study was to clarify the dominant hemisphere in the gaze processing that mediates attentional shift. A target localization task, with preceding non-predicative gaze cues presented to each visual field, was undertaken by 44 healthy subjects, measuring reaction time (RT). A face identification task was also given to determine hemispheric dominance in face processing for each subject. RT differences between valid and invalid cues were larger when presented in the left rather than the right visual field. This held true regardless of individual hemispheric dominance in face processing. Together, these results indicate right hemispheric dominance in gaze-triggered reflexive shifts of attention in normal healthy subjects.

Keywords: Gaze; Attention; Unilateral visual field presentation; Hemispheric dominance

1. Introduction

Eye gaze is a powerful communicative medium in human interaction. We have a tendency to direct attention to where another person is looking (Kingstone, Friesen, & Gazzaniga, 2000), and recent psychological studies have shown that this tendency—joint attention—occurs reflexively and automatically even if the gaze direction does not predict any relevant events in the environment (Driver et al., 1999; Friesen & Kingstone, 1998; Langton & Bruce, 1999).

Neurophysiological and neuropsychological studies have identified neural systems specializing in gaze processing (Emery, 2000). A single-cell recording in monkeys (Perrett et al., 1985) and lesion studies in monkeys and humans (Campbell, Heywood, Cowey, Regard, & Landis, 1990; Heywood & Cowey, 1992) have suggested involvement of the superior temporal sulcus (STS) in the perception of gaze direction. Another neurophysiological study showed involvement of the temporo-parietal projection from the STS to the intraparietal sulcus (IPS) in these processes (Harries & Perrett, 1991), while others have reported on defects in discrimination of gaze direction in a bilaterally amygdala-damaged patient (Young, Aggleton, Hellawell, Johnson, & Broks, 1995). Finally, recent neuroimaging studies have demonstrated involvement of neural networks including the STS (Puce, Allison, Bentin, Gore, & McCarthy, 1998; Wicker, Michel, Henaff, & Decety, 1998), IPS (Hoffman & Haxby, 2000), and amygdala (Kawashima et al., 1999) in gaze perception.

A variety of human cognitive functions, such as language processing, are dominantly processed in a single hemisphere. Such lateralization has been suggested regarding shift of attention in response to gaze direction by a recent study on two split-brain patients (Kingstone et al., 2000). Functional neuroimaging studies also suggest that

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changes in gaze direction preferentially activates the right STS in comparison to the left, although the difference did not reach significance (Puce et al., 1998; Wicker et al., 1998). These preliminary findings suggest that gaze perception may be a single hemisphere-dominant process in humans. In order to investigate this possibility in gaze processing mediating reflexive shifts of spatial attention, this study examined the reaction times (RTs) of healthy subjects in localizing targets with preceding non-predictive gaze cues presented to each visual field.

An additional purpose of this study was to investigate the relationship between gaze-triggered attentional shift and face perception. Kingstone et al. (2000) examined two split-brain patients and reported that the reflexive attentional shift is lateralized to the single hemisphere processing face perception. If this is the case with subjects having intact brain function, it would indicate that the dominant hemisphere for gaze-triggered reflexive shift of attention is lateralized to that involved with face processing. A face perception task was conducted in order to test this hypothesis.

2. Method

2.1. Subjects

Experiments were conducted at the Health and Medical Services Center of Shiga University. Forty-four healthy subjects initially participated in the study. The subjects were on no medication, and had no history of psychiatric, neurological, or ophthalmologic illness. All subjects were right-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971), and had normal or corrected-to-normal visual acuity. Average age was 19.0-year-old (*SD* 0.7, range 18–21). Informed consent was obtained after the procedure had been fully explained, but without revealing the goal of the experiments or the nature of the experimental conditions. The study protocol was approved by the institutional review board of the center.

2.2. Apparatus

Stimuli were presented on a flat type 19-in. CRT monitor. The refresh rate of the monitor was set to 100 Hz. The resolution of the monitor was 1024 × 768 pixels. The presentation of stimuli was controlled by SuperLab Pro ver. 2.0 (Cedrus, San Pedro, CA, USA) software. This software allowed for stimulus presentation within one screen refresh cycle (i.e. 10 ms) by setting up a new graphic page in the background of the screen. The RTs and accuracy measures were based on responses through a Cedrus RB-400 Response Box (Cedrus, San Pedro, CA, USA). Subjects were seated approximately 57.3 cm from the monitor, resting their heads on a head-rest to keep their heads fixed, with their bodies centered with respect to the monitor and the keys of the switch box. Conformity with these conditions was confirmed by the experimenter.

2.3. Gaze processing task

Valid (i.e. gaze direction toward targets) or invalid (i.e. gaze direction away from targets) gaze cues were randomly presented to either the left or the right visual field (LVR and RVF, respectively), alongside presentation of a straight-gazing face in the other visual field. A schematic representation of the face was adopted, as in previous studies (Friesen & Kingstone, 1998; Kingstone et al., 2000), to minimize extraneous complexities associated with real faces (e.g. face asymmetry, hair, gender, etc.). The face display consisted of a white background with a black line drawing of two round faces subtending 3.6°, located 3.9° away from the vertical axis of the screen.

The experiments were performed individually. Subjects were seated in an armchair and instructed to look at the monitor situated in front of them. The sequence of stimuli in each trial is illustrated in Fig. 1. The start of a trial was signaled by a warning alarm and the two faces with blank eyes were presented simultaneously on the CRT monitor. After 675 ms, the pupils in either the LVF or RVF were presented looking up or down at random. After 200 ms, the two faces were replaced by two target circles presented above or below until a response was made. The stimulus onset asynchrony (SOA) of 200 ms was adopted for maximum stability in performance as predicted from the results of previous studies using different SOAs (Driver et al., 1999; Friesen & Kingstone, 1998; Langton & Bruce, 1999), and because this SOA was appropriate for the unilateral visual field presentation paradigm. The inter-trial interval was 675 ms.

The subjects were instructed to indicate whether the targets appeared above or below the faces by pressing the upper or lower key on the switch box with either the left or right index finger. The position of hands in responding was counterbalanced among subjects. RTs were timed from the onset of target presentation, and measured in milliseconds.

At the beginning of the experiments, the subjects were given 16 practice trials. After the practice trials, five blocks of eight test trials were conducted twice. Then, subjects were requested to change hands for responding, and given another 16 practice trials. After the second block of practice trials, five blocks of eight test trials were conducted twice (all together 160 test trials). The order of the test trials was randomized within each block. There was a short break of about 15 s between blocks of the test and practice trials.

Before beginning the test, subjects were informed that it was important to fixate their eyes on the central fixation cross while it was presented, and that the gaze direction was not predictive of the location of the targets. They were also instructed to respond as quickly and accurately as possible to the targets.

2.4. Face perception task

The visual field demonstrating superiority in face processing was examined in each subject. The tasks were almost identical to those of Gazzaniga and Smylie (1983).

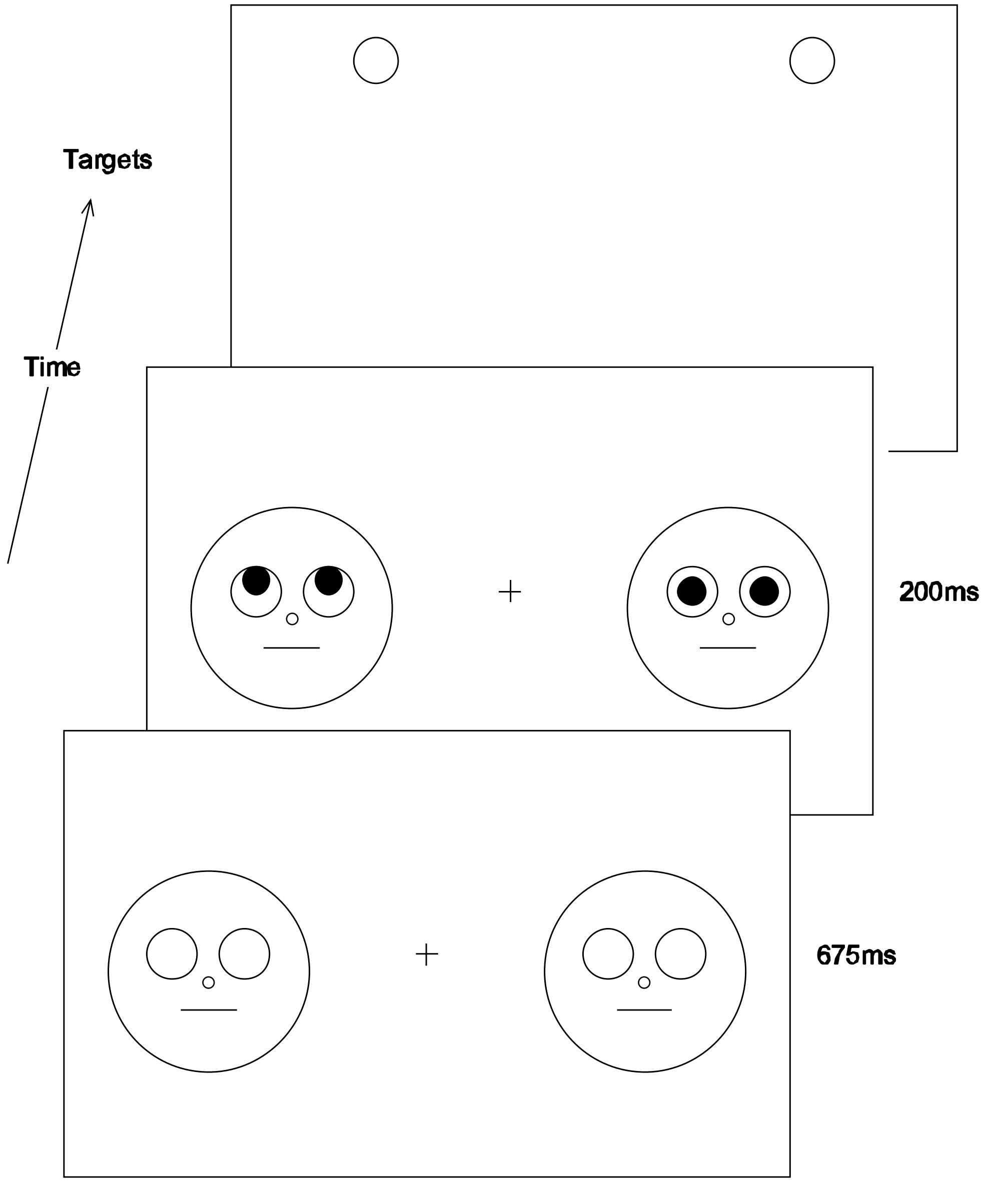

Fig. 1. Sample sequence of stimuli presented in the gaze-processing task. In this figure, the valid gazing-up cue is presented in the left visual field.

The stimuli were 20 unfamiliar Japanese faces (10 female, 10 male), presented in the LVF or RVF. The faces were oval shaped, minimizing extraneous clues (e.g., style of hair, outline of face). Pictures were devoid of apparent distinguishable features such as glasses or facial hair. Each face subtended 4° × 8° of visual angle. The nearest edge was 3° away from the central fixation.

The subjects, seated in front of a CRT monitor, were instructed to look at the fixation cross, which was black for the first 2000 ms, before turning red 500 ms before stimulus presentation. Then, the stimulus face was presented for 120 ms in either the left or right visual field at random. Following this stimulus presentation, a panel was presented with 10 different faces of the same gender. Subjects were instructed to select the same face as the stimuli from the set of 10 pictures and responses were recorded. The subjects were informed that each face might be projected more than once. They were instructed not to respond when they were unable to select any face on the panel.

Following 10 practice trials, the subjects were given 20 test trials. After a rest of about 30 s, another 20 test trials were conducted. The order of stimulus types was randomized in each block. Rates of correct response higher by more than 20% in presentations to one hemisphere than the other was regarded as demonstration of hemispheric superiority in face processing.

2.5. Data analysis

All data were analyzed with SPSS ver. 11.0J software (SPSS Japan Inc., Tokyo, Japan). Concerning the gaze processing task, mean RT of correct responses was first calculated for each experimental condition, excluding measurements beyond the mean ± 2 *SD* as artifacts. Then, RT differences between valid and invalid conditions were calculated as the measure of the shift of attention. The RT differences were analyzed using a $2 \times 2 \times 2$ repeated-measures ANOVA with hand of response (left-hand up/right-hand up), visual field (LVF/RVF), and position of targets (above/below) as within-subject factors.

To confirm the effect of hemispheric difference on RT, we subsequently analyzed mean RT using a 2×2 repeated-measures ANOVA with visual field (LVF/RVF), and validity (valid/invalid) as within-subject factors.

Concerning the face processing task, performance for LVF and RVF was compared using Student's paired *t* test on the number of correct responses calculated for each visual field. Then, the degree of hemispheric difference was obtained expressed as follows: (the number of correct responses in LVF − the number of correct responses in RVF)/(the total number of correct responses in LVF and RVF) $\times$ 100 (%). The value of this measure ranges from 100% to −100%. Positive values indicate right hemispheric dominance, and negative values indicate left hemispheric dominance. As stated before, right- and left-hemisphere superiority groups were defined as subjects exhibiting values exceeding 20% or less than −20% on this measure, respectively.

To examine whether the gaze-triggered reflexive shift of attention was influenced by hemispheric dominance in face processing, RT data was re-analyzed using face-processing hemispheric dominance as an additional between-subject factor. RT differences were analyzed using a $2 \times 2 \times 2 \times 2$ ANOVA with hand of response (left-hand up/right-hand up), visual field (LVF/RVF), and position of targets (above/below) as within-subject factors, and face-processing hemispheric dominance (left hemispheric dominance/right hemispheric dominance) as a between-subject factor.

An analysis of covariance (ANCOVA) was also conducted. The RT differences were analyzed using a $2 \times 2 \times 2 \times 2$ ANCOVA with hand of response (left-hand up/right-hand up), visual field (LVF/RVF), and position of targets (above/below) as within-subject factors, and the face-processing hemispheric-dominance score as the covariate.

3. Results

Of the 44 subjects who participated in the study, five were excluded from analysis because of non-compliance to the instructions (in one), a significant difference in vision between eyes (in one), and exceptionally slow responses (i.e. beyond mean + 2*SD* of the whole data set, in three subjects). As a result, data from the remaining 39 (7 males and 32 females) subjects were analyzed. Preliminary analyses revealed no significant effect or interactions regarding gender. Therefore, the following analyses were conducted using data collapsed across gender.

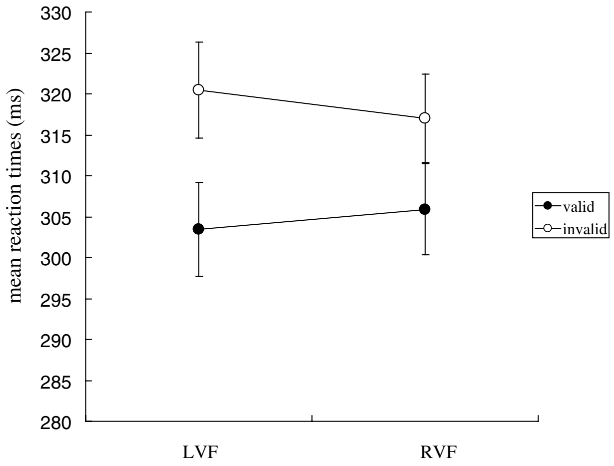

Fig. 2. Mean reaction times (with standard error) to valid and invalid cues in the gaze-processing task.

The mean RT findings are shown in Fig. 2. Subjects responded about 17 and 11 ms faster when the gaze cue was presented in the LVF and RVF, respectively, in the valid than invalid condition, which is consistent with results from previous studies using a similar paradigm. Error rates were very small (less than 1%), and there was no apparent speed-accuracy trade-off. The ANOVA on RT differences revealed a significant main effect of visual field ($F_{(1,38)} = 4.4$, $p < .05$). There were no other significant main effects or interactions with visual field. These results indicate that LVF presentation produced larger RT differences between valid and invalid stimuli than RVF presentation.

The subsequent 2 (visual field: LVF/RVF) $\times$ 2 (validity: valid/invalid) ANOVA on mean RT revealed significant interaction of visual field and validity ($F_{(1,38)} = 4.4$, $p < .05$), confirming the above analysis on RT differences. The main effect of validity was also significant ($F_{(1,38)} = 134.8$, $p < .001$).

In the face processing task, the mean number of correct responses were 4.0 (*SD* 2.3) and 4.0 (*SD* 2.2) for the RVF and LVF presentations, respectively. Difference between visual fields in terms of correct recognition was not significant ($t_{(38)} = 0.1$, $p > .1$, *n.s.*). Regarding hemispheric dominance in face perception (based on the face identification task), the left and right dominant groups consisted of 9 and 11 subjects, respectively, with the remaining 19 showing no apparent hemispheric dominance. Data was then re-analyzed for the 20 subjects with clear hemispheric dominance. The mean RT (*SD*) was 291.7 (22.6), 306.4 (22.4), 297.9 (18.3), and 303.6 (25.2) for valid LVF, invalid LVF, valid RVF, and invalid RVF presentations, respectively, in the left dominance group, and 303.4 (35.8), 320.8 (39.3), 307.8 (36.8), 312.8 (31.8), respectively, in the right dominance group.

The 2 (hand of response: left-hand up/right-hand up) $\times$ 2 (visual field: LVF/RVF) $\times$ 2 (position of targets: above/below) $\times$ 2 (face-processing hemispheric dominance: left hemispheric dominance/right hemispheric dominance) ANOVA for RT differences showed that the main effect of visual field remained significant ($F_{(1,18)} = 7.4$, $p < .05$) even with addition of the extra between-subject factor of face-processing hemispheric dominance, with no interaction between visual field and face-processing hemispheric dominance. No other main effects or interactions were significant.

The 2 (hand of response: left-hand up/right-hand up) × 2 (visual field: LVF/RVF) × 2 (position of targets: above/below) ANCOVA for RT differences using face-processing hemispheric dominance scores as the covariate showed that only the main effect of visual field remained significant ($F_{(1,37)} = 4.2, p < .05$).

4. Discussion

The current study investigated hemispheric dominance in the reflexive shift of attention in response to perceived gaze directions, using a target localization task in an RT paradigm. The result showed that the cuing effect was significantly larger for the LVF than RVF presentation, which was not attributable to a speed-accuracy trade-off. These results indicate a right hemispheric dominance in gaze-triggered attentional shifts. Right hemispheric superiority in gaze processing has been suggested by previous neuropsychological (Campbell, Landis, & Regard, 1986) and neuroimaging studies (Puce et al., 1998; Wicker et al., 1998). The results from those studies, however, were inconclusive, and no previous studies have specifically examined hemispheric dominance in the gaze-triggered reflexive shift of attention in normal subjects. To our knowledge, the present study is the first to demonstrate right hemispheric dominance in the gaze-triggered reflexive shift of attention in a normal human population.

It is of interest that the main effect of visual field remained significant even when taking face-processing hemispheric dominance into consideration, indicating right hemispheric dominance in the gaze-triggered reflexive shift of attention regardless of the hemispheric dominance in face perception. This suggests that the cerebral regions that process gaze directions may not be entirely the same as those involved in the face processing demanded by the face identification task. This appears consistent with recent findings that suggest the involvement of different neural substrates in gaze processing and face perception. For example, an fMRI study revealed that the fusiform gyrus was involved in face perception (Kanwisher, McDermott, & Chun, 1997) and another fMRI study showed that the STS region was more active in response to averted gazes than straight gazes, whereas the fusiform gyrus did not differentiate these conditions (Hoffman & Haxby, 2000). Such neuroimaging findings (e.g., Hoffman & Haxby, 2000) raise the possibility that the primary neural substrate may be the STS for gaze processing and the fusiform gyrus for face perception.

There is a study examining two split-brain patients reporting that the processing of gaze directions and upright faces were lateralized to the same hemisphere (Kingstone et al., 2000). In the study, while gaze directions both with and without other face components produced gaze-triggered shift of attention in one, but not the other, hemisphere, gaze directions lost their effect when presented as part of an inverted face. These findings provide evidence pointing to a common laterality for gaze and face processing, as well as the import of face components on gaze processing. Our study, on the other hand, suggests right hemispheric dominance in gaze processing even in (right-handed) subjects who process faces primarily in the left hemisphere. One possible explanation for this inconsistency in results of the two studies might be the difference in type of face processing between subjects. In other words, the strategy for face discrimination might depend, at least in part, on cultural factors and other demographic variables. Another reason may be the lack of dominance in face identification in a considerable proportion of our subjects (i.e. 19 out of 39). This seems to suggest the possibility that, unlike gaze processing of faces, the strategies of face identification may be heterogeneous among individuals. Therefore, the findings from the present study do not necessarily exclude the possibility of their portraying a relationship between gaze-triggered attentional shift and a specific type of face perception. In monkeys, neuroanatomical studies have found a connection between the STS and inferior temporal regions (Perrett, Oram, & Ashbridge, 1998; Seltzer & Pandya, 1978), which have been suggested as being homologous to the human STS and fusiform gyrus, respectively. In humans, similar neural or functional connections might exist between brain regions for processing gaze and other face components.

Our results from the face perception task did not reveal right hemispheric dominance. This seems inconsistent with previous experimental studies on normal subjects (e.g., Moscovitch & Klein, 1980) and neuropsychological prosopagnosic patients (e.g., Benton, 1980) reporting right hemispheric dominance in facial recognition. However, other studies have reported bilateral hemispheric involvement in face recognition (e.g., Magnussen, Sunde, & Dyrnes, 1994; Hamsher, Levin, & Benton, 1979), calling for further research to resolve such inconsistencies regarding hemispheric asymmetry in face processing.

While the current study focused on reflexive responses to gaze stimuli, previous functional imaging studies have primarily examined the non-reflexive components of processing facial parts including the eyes. A lack of joint attention is a well-documented feature of autism, a pathological condition in which abnormality in neural development has consistently been noted in the amygdala-limbic regions (Bauman & Kemper, 1985, 1994). Considering these findings on autism, there is a possibility that subcortical structures other than the STS and fusiform gyrus (such as the amygdala) may be involved in the reflexive or automatic processing of gaze stimuli, warranting functional imaging studies to clarify the neural mechanisms that mediate gaze-triggered reflexive shifts of attention.

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