# Research Report

# REFLEXIVE JOINT ATTENTION DEPENDS ON LATERALIZED CORTICAL CONNECTIONS

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**Abstract**—*Joint attention, the tendency to spontaneously direct attention to where someone else is looking, has been thought to occur because eye direction provides a reliable cue to the presence of important events in the environment. We have discovered, however, that adults will shift their attention to where a schematic face is looking—even when gaze direction does not predict any events in the environment. Research with 2 split-brain patients revealed that this reflexive joint attention is lateralized to a single hemisphere. Moreover, although this phenomenon could be inhibited by inversion of a face, eyes alone produced reflexive shifts of attention. Consistent with recent functional neuroimaging studies, these results suggest that lateralized cortical connections between (a) temporal lobe subsystems specialized for processing upright faces and gaze and (b) the parietal area specialized for orienting spatial attention underlie human reflexive shifts of attention in response to gaze direction.*

Where other people look can reveal where they are attending, and thus indicate sources of potential interest or danger in the environment. It is perhaps not surprising that human eye morphology (sclerato-iris ratio) may have evolved to allow easy discrimination of small shifts in the eye direction of another individual (Kobayashi & Kohshima, 1997), and that noticing eye direction begins to develop early in humans. Infants as young as 2 to 3 months look preferentially at the eyes of a schematic face (Maurer, 1985), and by 12 months, infants look reliably to where someone else is looking, regardless of whether a shift in gaze is accompanied by a turn of the face (Corkum & Moore, 1995; Scaife & Bruner, 1975; see also Hood, Willen, & Driver, 1998, for data suggesting that infants as young as 10 weeks can follow gaze shifts alone). Indeed, it has been suggested that this emergence of joint attention plays a key role in the development of social cognition (Baron-Cohen, 1995; Tantam, 1992). It also appears that joint attention is fundamental to adult behavior. Recent work by ourselves and others has shown that neurologically intact adults will attend to where someone else is looking, even if a shift in gaze or a turn of the face does not predict where a target will appear (Driver et al., in press; Friesen & Kingstone, 1998; Langton & Bruce, in press). Such shifts in spatial attention produce shorter response latencies for target stimuli that appear at the location that the eyes or face are directed toward.

The goal of the present study was to examine the brain mechanisms underlying this reflexive joint attention. We reasoned that reflexive attention to gaze direction might depend critically on cortical pathways. Considerable evidence now supports the idea that separate cortical systems underlie the localization and identification of objects. The ventral projection from occipital cortex to temporal cortex is crucial for processing what an object is (Grady et al., 1992; Haxby et al., 1991), and the dorsal projection from occipital cortex to the parietal lobe is critical for processing where an object is and directing spatial attention to it (Corbetta, Shulman, Miezin, & Petersen, 1995; Grady et al., 1992; Haxby et al., 1991). There is also evidence that within the temporal cortex, specific sites are sensitive to the processing of biologically important stimuli such as eyes and faces (Campbell, Heywood, Cowey, Regard, & Landis, 1990; Kanwisher, McDermott, & Chun, 1997; Perrett et al., 1985; Puce, Allison, Gore, & McCarthy, 1995), with advantages for upright-face processing lateralized to a single hemisphere in most humans and nonhuman primates (Gazzaniga & Smylie, 1983; Hamilton & Vermeire, 1988; Hillger & Koenig, 1991; Young, Hay, & McWeeny, 1985).

Our hypothesis was that reflexive attention in response to gaze direction reflects an interaction between neurons in the temporal cortex of the hemisphere specialized for processing faces and eyes and neurons in the parietal cortex responsible for orienting spatial attention. Nonhuman primate studies have provided both physiological and anatomical evidence that there exists a strong connection between the temporal and parietal lobes (Harries & Perrett, 1991). Because face processing in humans is lateralized to one hemisphere, one might expect that only the hemisphere specialized for face processing would shift spatial attention quickly and automatically in response to gaze direction. To test the performance of each hemisphere separately, we examined 2 patients who have had their cerebral hemispheres disconnected because of intractable epilepsy: patient J.W. (Experiments 1–3) and patient V.J. (Experiments 4–6).

The first split-brain patient, J.W., is right-handed, with both verbal and written language output lateralized to the left hemisphere. J.W. can orient spatial attention with either hemisphere (Kingstone, Enns, Mangun, & Gazzaniga, 1995; Luck, Hillyard, Mangun, & Gazzaniga, 1989), but is known to have a right-hemisphere advantage for processing upright faces (Gazzaniga & Smylie, 1983). A strong prediction was that for J.W., gaze direction of an upright face would trigger reflexive shifts of attention by the right hemisphere, but not by the left hemisphere.

## METHOD

### Subjects

Callosotomy patient J.W. is a 44-year-old male who suffered from intractable epilepsy beginning in 1972. J.W. underwent a two-stage microneurosurgical section of his corpus callosum (verified by magnetic resonance imaging, MRI) in 1979. Postoperatively, both of J.W.'s hemispheres demonstrated the capacity to comprehend language, although verbal and written language output was lateralized to the left hemisphere. This patient has participated in numerous behavioral investigations and is well known for holding central fixation on

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instruction. A detailed description of this subject has previously been published (Gazzaniga, Nass, Reeves, & Roberts, 1984).

Callosotomy patient V.J. is a 44-year-old female who had intractable epilepsy since 1969. V.J. underwent a two-stage section of her corpus callosum (MRI verified) in 1994. See Baynes, Eliassen, Lutsep, and Gazzaniga (1998) for a recent and detailed description of this subject.

Informed consent was obtained after the nature and possible consequences of the study were explained. All experiments were performed in compliance with the relevant laws and institutional guidelines of Dartmouth College and the University of Alberta, and the experiments were approved by each institution's ethics review committee.

### Stimuli

Stimuli were controlled by an Apple Macintosh PowerBook 180c computer connected to a 14-in. Apple Macintosh color monitor set to black and white. Each stimulus face measured 5.2° high and 3.1° wide, and was centered 2.4° to the left or right of a central fixation cross (subtending 0.3°). The eyes subtended 0.8°, and the center of each eye was 0.6° to the left or right of the vertical axis of the face and 0.3° above the horizontal axis of the face. The nose subtended 0.2°. The mouth was 1.6° in length and was centered 0.5° below the nose. The pupils subtended 0.5° and were either centered in the eyes or both just touching the top or bottom of the eyes. The target asterisk subtended 0.7°, and always appeared 4.2° away from the fixation cross.

### Procedure

The experimenter ensured that each subject was centered with respect to the screen and keyboard, and monitored central fixation, which was held without difficulty throughout each block of trials. In each experiment, subjects received 20 practice trials followed by two sets of 10 blocks, each block consisting of 72 test trials, for a total of 1,440 test trials. Subjects initiated each block with a key press and rested between blocks. Gaze direction, target location, and target onset time were selected randomly on each trial. Subjects were informed repeatedly, and understood, that gaze direction did not predict where the target would appear. They were strongly encouraged to respond as quickly and as accurately as they could, pressing a left-hand key ("Z") when the target was presented to the left visual field (LVF), and a right-hand key ("/") when the target was in the right visual field (RVF).

Response time (RT) was measured in milliseconds and timed from target onset. Anticipations (RT < 100 ms) and incorrect key selections were classified as errors and excluded from RT analyses. Latency and accuracy data were subjected to an analysis of variance with visual field of the target, gaze-target stimulus onset asynchrony (SOA), and congruency of gaze direction and target location as factors. The straight-ahead gaze provided a baseline condition for assessing general foreperiod effects and RT differences between the hemispheres. On both these counts, the baseline data paralleled those observed for the directional cues. Planned contrasts tested for specific differences in RT and accuracy measures. There were no systematic differences in accuracy, and in no condition is the reported RT effect contradicted by the accuracy data.

## RESULTS

### Experiments 1–3: Patient J.W.

In Experiment 1, J.W. was presented with two schematic faces that flanked a central fixation cross (Fig. 1). Target onset could occur above or below the schematic face in either visual field. The faces gazed up, down, or straight ahead 100 ms or 600 ms prior to target onset. J.W. fixated the central cross and indicated with a left- or right-hand key press whether the target (an asterisk) appeared in the LVF or RVF, respectively. Note that gaze direction did not predict target location.
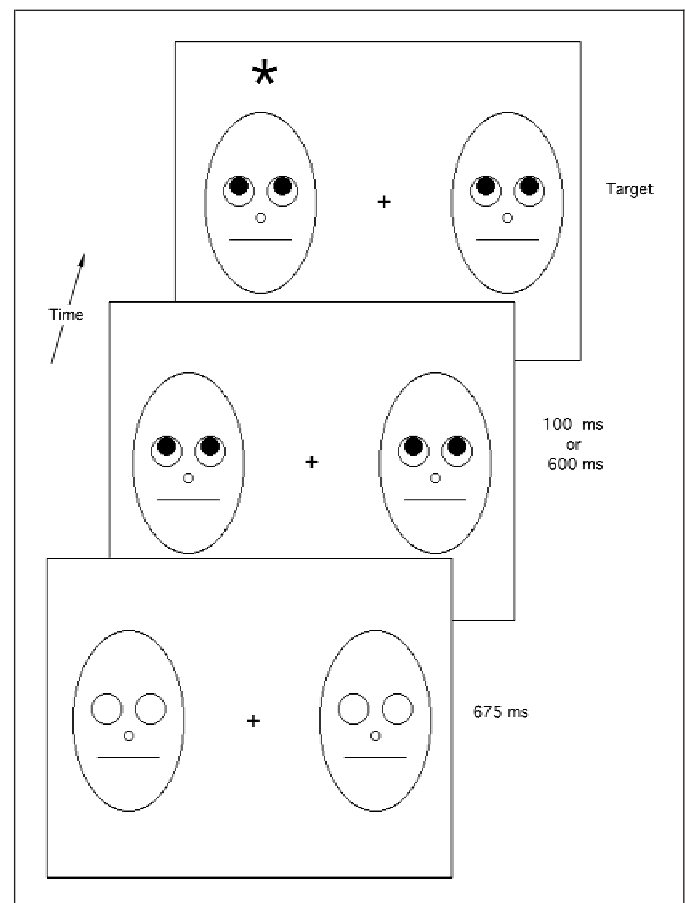


**Fig. 1.** Example sequence of events. Two faces (upright in Experiments 1 and 4; inverted in Experiments 2 and 5) or two pairs of eyes (Experiments 3 and 6) were presented concurrently to the left of a central fixation cross (left visual field, or LVF) and to the right of the cross (right visual field, or RVF). The eyes remained blank for 675 ms, and then black dots (the "pupils") were presented 100 ms or 600 ms before a target (the asterisk) appeared. The faces, pupils, and target remained on the screen until a response was made or 2,700 ms had elapsed, whichever came first. The intertrial interval was 675 ms. The task was to maintain central fixation and to press a left-hand key when the target was presented to the LVF (right hemisphere) and a right-hand key when the target was in the RVF (left hemisphere). Responses were speeded. Gaze direction did not predict target location. In the present example, gaze direction in the LVF is directed toward the target.

Figure 2a shows that there was a large effect of gaze direction in the LVF (right hemisphere) at the 100-ms SOA ($p < .02$), with responses 47 ms faster when gaze was congruent versus incongruent with the target location. This effect disappeared when the SOA was 600 ms ($p > .50$). There was no effect of gaze direction in the RVF (left hemisphere) at either the 100- or the 600-ms SOA ($ps > .50$). For both visual fields and gaze conditions, RT was significantly longer at the 100-ms SOA than at the 600-ms SOA (all $ps < .001$), reflecting a foreperiod effect across cue-target interval. Finally, RT was longer for LVF than for RVF displays ($p < .001$).

The finding that a nonpredictive shift in gaze by a schematic face will trigger, within 100 ms, a reflexive shift of attention to the location where gaze is directed replicates our previous finding with neurologically intact subjects (Friesen & Kingstone, 1998). That this phenomenon is short-lived, and disappears within 1,000 ms, is consistent with reflexive attention and has also been demonstrated previously (Driver et al., in press; Friesen & Kingstone, 1998; Langton & Bruce, in press). The new finding is that in J.W., reflexive attention to gaze direction is lateralized to the right hemisphere, consistent with this hemisphere's specialization for processing upright faces.

It has been shown that inverting a face can attenuate or abolish right-hemisphere advantages for upright-face processing (Hillger & Koenig, 1991; Leehey, Carey, Diamond, & Cahn, 1978). Therefore, in Experiment 2, we retested J.W. using the same procedure as before, but with the stimulus displays inverted. The results, shown in Figure 2b, suggest that there might have been a small effect of gaze direction in the LVF (right hemisphere) at the 100-ms SOA; however, this effect fell far short of significance ($p > .20$), as did all other effects involving gaze direction ($ps > .50$). As before, the foreperiod effect between 100 ms and 600 ms was significant for both visual fields and gaze conditions (all $ps < .001$).

The results of Experiments 1 and 2 indicate that for J.W., reflexive orienting to a noninformative gaze shift is a right-hemisphere process that occurs for upright faces (Experiment 1) but not for inverted faces (Experiment 2). This interaction between gaze processing and more general face processing is consistent with evidence from nonhuman primate studies, which have shown that the superior temporal sulcus (STS) contains cells that are sensitive to gaze direction and that receive projections, and pool outputs, from cells sensitive to faces in the inferior temporal (IT) cortex (Perrett, Oram, & Wachsmuth, 1998; Seltzer & Pandya, 1978). Indeed, the results of Experiment 2 suggest that gaze processing might actually depend on face processing, an interpretation consistent with recent evidence that face inversion reduces the activation of cell populations tuned to faces in the STS and IT (Perrett et al., 1998; Tanaka, Saito, Fukada, & Moriya, 1991).

Experiment 3 directly tested whether reflexive orienting to gaze direction is dependent on face processing. This experiment was identical to Experiments 1 and 2, with the exception that all face features, except the eyes, were removed from the schematic faces. Thus, only the two pairs of eyes were presented to J.W. Figure 2c shows that there was an effect of gaze direction in the LVF (right hemisphere) at the 100-ms SOA ($p < .05$), with responses 83 ms faster when gaze was congruent versus incongruent with the target location. This effect disappeared when the SOA was 600 ms ($p > .50$). There was no effect of gaze direction in the RVF (left hemisphere) at either the 100- or the 600-ms SOA ($ps > .50$). Foreperiod effects were significant, as before (all $ps < .001$).

These results for eyes presented alone replicate those found in Experiment 1 for upright faces. Taken together, the findings indicate that although reflexive orienting to gaze direction can interact with processing of face orientation, it is not dependent on face processing—a pair of gazing eyes is sufficient to produce the effect.

Each of these three experiments with J.W. reveals something new about the relationships between gaze and attentional orienting, or between gaze and face processing. In Experiment 1 (upright faces), we found that reflexive attention to gaze is lateralized to J.W.'s face-processing hemisphere. Experiment 2 (inverted faces) demonstrated that reflexive attention to gaze can be inhibited by a manipulation that compromises face processing. This result suggested that gaze processing might be dependent on face processing. However, Experiment 3 (eyes only) showed that although reflexive attention to gaze can be affected by face processing, it does not depend on face processing.

## Experiments 4–6: Patient V.J.

Are these effects specific to the single split-brain patient J.W.? And are they specific to the right hemisphere? To test these questions, we conducted three more experiments, this time with split-brain patient V.J., whose pattern of lateralization is different from J.W.'s. As is the case with J.W., both of V.J.'s hemispheres can orient attention. However, unlike J.W., V.J. is left-handed, and has anomalous language lateralization, with verbal output lateralized to the left hemisphere and written output lateralized to the right hemisphere. And most important, V.J.'s upright-face processing advantages are lateralized to the left hemisphere.

Experiments 4 through 6 with V.J. were identical to Experiments 1 through 3 with J.W. The results, presented in Figure 3, replicate those observed for J.W., with the exception that the attention effects were isolated to the RVF (left hemisphere). Figure 3a shows that for upright faces, there was a large effect of gaze direction in the RVF (left hemisphere) at the 100-ms SOA ($p < .02$), with responses 45 ms faster when gaze was congruent versus incongruent with the target location. This effect disappeared with the 600-ms SOA ($p > .50$). There was no effect of gaze direction in the LVF (right hemisphere) at either the 100- or the 600-ms SOA ($ps > .50$). Figure 3b shows that inverting the faces abolished all effects of gaze direction ($ps > .10$). And Figure 3c shows that when eyes alone were presented, there was an effect of gaze direction in the RVF (left hemisphere) at the 100-ms SOA ($p < .05$), with responses 49 ms faster when gaze was congruent versus incongruent with the target location. This effect disappeared with the 600-ms SOA ($p > .50$). There was no effect of gaze direction in the LVF (right hemisphere) at either the 100- or the 600-ms SOA ($ps > .20$). In all the experiments, foreperiod effects were reliable only for RVF presentations (all $ps < .001$), and RT was always longer for RVF than LVF displays (all $ps < .001$).

These data indicate that, as is the case for J.W., V.J.'s reflexive orienting to gaze direction is lateralized to the hemisphere specialized for processing upright faces—in this case, the left hemisphere. Thus, our finding with J.W. that reflexive joint attention is lateralized to a single hemisphere was replicated with V.J. And her data demonstrate that reflexive joint attention is not specific to the right hemisphere.

## DISCUSSION

Together, the data indicate that reflexive orienting to gaze direction is lateralized to the hemisphere specialized for processing upright
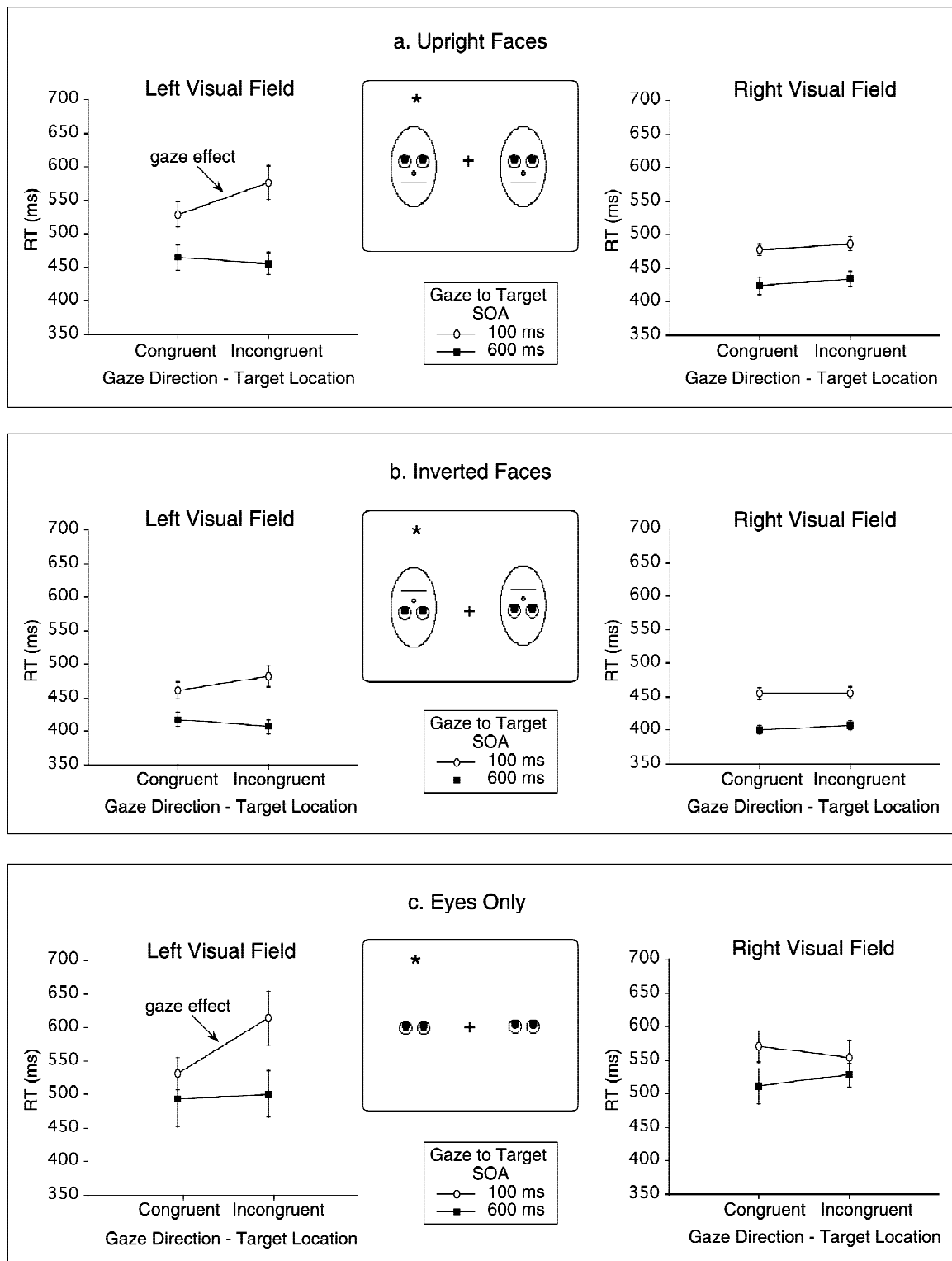
**Fig. 2.** J.W.'s results for Experiment 1 (a; upright faces), Experiment 2 (b; inverted faces), and Experiment 3 (c; eyes only). The illustration in the center of each panel shows target onset (an asterisk) congruent with the gaze direction in the left visual field. The graphs show correct response time (RT) and standard error performance in milliseconds when a target was presented to the left visual field (right hemisphere) or the right visual field (left hemisphere). Results are shown separately for the 100-ms and 600-ms stimulus onset asynchronies (SOA).
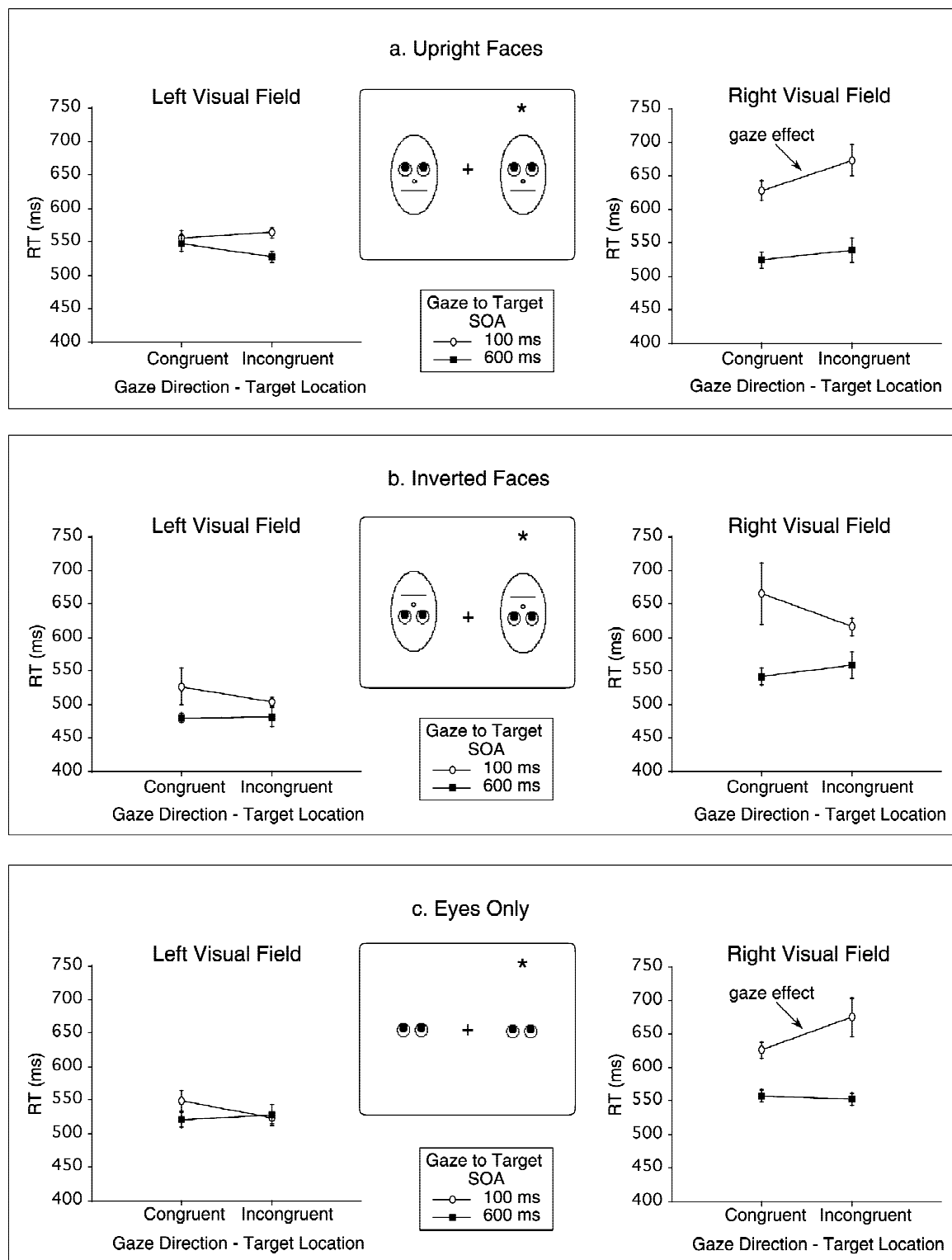
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**Fig. 3.** V.J.'s results for Experiment 4 (a; upright faces), Experiment 5 (b; inverted faces), and Experiment 6 (c; eyes only). The illustration in the center of each panel shows target onset (an asterisk) congruent with the gaze direction in the right visual field. The graphs show correct response time (RT) and standard error performance in milliseconds when a target was presented to the left visual field (right hemisphere) or the right visual field (left hemisphere). Results are shown separately for the 100-ms and 600-ms stimulus onset asynchronies (SOA).

faces. In J.W. that is the right hemisphere, and in V.J. that is the left hemisphere. The fact that inverting a face can abolish any effects of gaze direction demonstrates that face processing can have a profound effect on gaze processing. This finding is consistent with the idea that cells sensitive to gaze direction in the STS pool outputs from cells sensitive to faces in IT. Our data suggest that when an inverted face is presented, face-sensitive cells in IT may provide inhibitory output either to eye cells in IT or to gaze cells in STS. However, it is important to note that the lateralization of reflexive orienting to gaze direction is not dependent on upright-face processing; lateralized reflexive shifts of attention occurred even when eyes alone were presented to the split-brain patients. This suggests that when there is no information that conflicts with the interpretation of a pair of eyes in an upright face, gaze processing in the STS proceeds unimpeded, on the basis of input from eye-sensitive cells in IT.

The present study also provides strong evidence that gaze processing is lateralized to the hemisphere (left or right) that is specialized for processing upright faces. The results support and extend recent functional neuroimaging studies suggesting that gaze and upright-face processing are preferentially lateralized to the right hemisphere (Puce, Allison, Bentin, Gore, & McCarthy, 1998; Wicker, Michel, Henaff, & Decety, 1998). Moreover, our data suggest that reflexive orienting to gaze direction reflects a rapid cortical exchange of information between the temporal and parietal lobes, with the temporal cortex responsible for processing face and gaze information, and the parietal cortex responsible for orienting spatial attention on the basis of this information. This interpretation dovetails with the nonhuman-primate research demonstrating a tight link between these two cortices (Harries & Perrett, 1991) and with functional neuroimaging investigations (Hoffman & Haxby, 1999; Wicker et al., 1998) indicating that shifts in gaze direction activate temporal and parietal cortices. Finally, our data demonstrate that within the temporal lobe, gaze processing can be affected by general face processing (effects of gaze direction can be abolished by inverting a face), but gaze processing is not dependent on general face processing (effects of gaze direction can occur when the eyes are presented alone). Determining how this interaction is realized at a neuronal level will be an exciting challenge for future investigation.

It is important to note that our data do not indicate simply that any index of attentional orienting to gaze direction will be lateralized to the hemisphere that is preferentially biased to process face and gaze information. Rather, the key is whether the attentional orienting is reflexive (triggered by a nonpredictive gaze cue, as in the present series of experiments) or volitional (triggered by a predictive cue; see Danziger & Kingstone, in press, for a recent review of exogenous vs. endogenous orienting).

To demonstrate this point, we conducted a control study wherein we repeated the procedure used in Experiment 1 with patient J.W. but indicated that gaze direction was predictive of where the target stimulus was likely to appear (i.e., in either visual field, the target appeared at a gazed-at location on 75% of the trials and at a non-gazed-at location on 25% of the trials). All other aspects of the study were the same as in Experiment 1 (e.g., gaze direction and target field varied randomly from trial to trial).

The results, presented in Figure 4, revealed that there was a significant effect of gaze direction in both visual fields at the 100-ms SOA (31 ms in the LVF, 22 ms in the RVF) and at the 600-ms SOA (29 ms in the LVF, 33 ms in the RVF), all $ps < .02$. Foreperiod effects were highly reliable, and RT was always longer for LVF than for RVF displays, all $ps < .001$. These data indicate that both hemispheres oriented attention volitionally to the predicted gazed-at location across
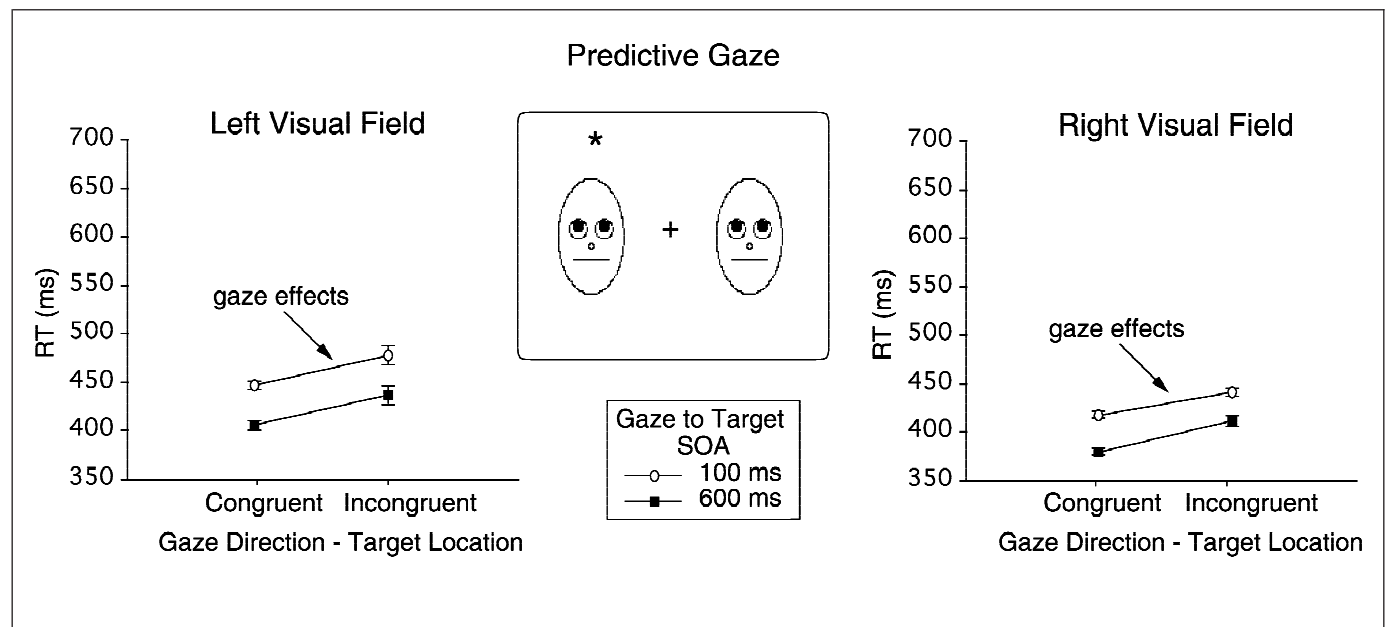


**Fig. 4.** J.W.'s results for the control experiment, in which target onset occurred at a gazed-at location on 75% of the trials. The illustration in the center shows target onset (an asterisk) congruent with the gaze direction in the left visual field. The graphs show correct response time (RT) and standard error performance in milliseconds when a target was presented to the left visual field (right hemisphere) or the right visual field (left hemisphere). Results are shown separately for the 100-ms and 600-ms stimulus onset asynchronies (SOA).

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both SOAs. This control study agrees with previous split-brain studies indicating that both hemispheres can orient attention volitionally when an attentional cue predicts target location (e.g., Enns & Kingstone, 1997; Holtzman, Volpe, & Gazzaniga, 1984; Kingstone, Grabowecky, Mangun, Valsangkar-Smyth, & Gazzaniga, 1997), and with studies demonstrating that the attentional effects of volitional orienting span short and long SOAs (Danziger & Kingstone, in press; Kingstone et al., 1997). Thus, the lateralization of reflexive attention to nonpredictive gaze direction observed in Experiments 1 through 6 reflects an interaction between gaze processing and the predictive (attentional) value of the gaze cue.

Finally, it is worth noting that we (Enns & Kingstone, 1997; Kingstone et al., 1997) have found that in some attentional tasks, hemispheric specialization reflects cortical competition for shared subcortical resources that each hemisphere might need. In other words, the "specialization" is resident not in the hemisphere per se, but in the degree of privilege granted each hemisphere in its communication with shared subcortical resources. It is extremely unlikely, however, that competition of this sort is responsible for our finding that reflexive orienting to nonpredictive gaze direction is lateralized to a single hemisphere, because without exception the findings of competition occurred when attentional orienting was volitional and not reflexive. The evidence with gaze direction has produced precisely the opposite pattern of results; that is, both hemispheres orient attention volitionally in response to gaze direction, but only one hemisphere orients attention reflexively to gaze direction. Nevertheless, one could test this issue in at least two ways. One test would involve comparing performance using the present bilateral displays (in which cortical competition could occur) with performance when a unilateral display of nonpredictive gaze is presented to a single hemisphere (which would preclude any hemispheric competition). An alternative test would involve presenting bilateral and unilateral displays of nonpredictive attentional cues that are not biologically relevant, such as arrows or abrupt peripheral onsets, to assess whether reflexive orienting is observed in only a single hemisphere. It should be noted, however, that previous studies using nonpredictive peripheral cues of this type have consistently found that both hemispheres of split-brain patients can orient attention reflexively and in parallel (e.g., Kingstone et al., 1997).

Does shifting of attention in response to nonpredictive gaze direction represent a special form of reflexive orienting? We think that it does for at least two reasons. First, it is well established that socially irrelevant stimuli, such as abrupt onsets and luminance changes, produce a bimodal RT pattern: facilitation at the cued location at a short cue-target SOA followed by inhibition at the cued location at a long cue-target SOA (e.g., Danziger & Kingstone, in press; Kingstone & Pratt, in press). To date, reflexive orienting to nonpredictive gaze direction has never been found to produce inhibition at the gazed-at (cued) location (see the present study as well as Driver et al., in press; Friesen & Kingstone, 1998; Langton & Bruce, in press). Second, it is well established that the bimodal RT pattern produced by socially irrelevant stimuli depends largely on the involvement of subcortical brain mechanisms, particularly the superior colliculus, that are shared between the disconnected hemispheres of split-brain patients (Rafal, Calabresi, Brennan, & Sciolto, 1989; Rafal, Henik, & Smith, 1991). Our data, however, suggest that reflexive joint attention depends largely on the involvement of cortical pathways that are lateralized, and not on subcortical pathways that are shared between the hemispheres.

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