Perceived gaze direction in faces and spatial attention: a study in patients with parietal damage and unilateral neglect

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Abstract

Perceived gaze in faces is an important social signal that may influence orienting of attention in normal observers. Would such effects of gaze still occur in patients with right parietal damage and left neglect who usually fail to attend to contralesional space? Two experiments tested for effects of perceived gaze on visual extinction. Face or shape stimuli were presented in the right, left, or both hemifields, with faces looking either straight ahead or toward the opposite field. On bilateral trials, patients extinguished a left shape much less often when a concurrent right face looked leftward rather than straight ahead. This occurred, even though gaze was not relevant to the task and processing of facial signals implied attention to a competing ipsilesional stimulus. By contrast, rightward gaze in faces presented on the left side had no effect on extinction, suggesting that gaze cues are not extracted without attention. Two other experiments examined effects of perceived gaze on the detection of peripheral targets. Targets appeared at one of four possible locations to the right or left of a central face looking either toward the target location, another location on the same side, the opposite side, or straight ahead. Face and gaze were not relevant to the task and not predictive of target location. Patients responded faster when the face looked toward the target on both the contralesional and ipsilesional sides. In contralesional space, gaze allowed shifting of attention in a specific quadrant direction, but only to the first target along the scan path when there were different possible locations on the same side. By contrast, in intact ipsilesional space, attention was selectively directed to one among different eccentric locations. Control experiments showed that symbolic arrow cues did not produce similar effects. These results indicate that even though parietal damage causes spatial neglect and impairs the representation of location on the contralesional side, perceived gaze in faces can still trigger automatic shifts of attention in the contralesional direction, suggesting the existence of specific and anatomically distinct attentional mechanisms. © 2002 Elsevier Science Ltd. All rights reserved.

Keywords: Spatial attention; Spatial neglect; Face; Gaze

1. Introduction

Attention plays a major role in perception and cognition, allowing to search for, detect and learn about relevant sensory stimuli [35,40]. Hemispatial neglect entails a severe deficit in attention and awareness due to unilateral brain damage, particularly in the right inferior parietal lobe [24,35]. These patients may fail to notice and orient to stimuli on the side contralateral to their lesion, even though primary sensory pathways are often intact and still capable of some residual processing [5,12,52]. Perceptual extinction is an important sign of inattention associated with neglect, in which the patients can detect a single stimulus on the contralesional side but ignore it when simultaneously presented with a competing stimulus on the ipsilesional side [11,24]. Some investigators however suggested that extinction might reflect a subtle deficit in sensory afferent rather than a disorder of attention [4,16] and occasionally dissociate from other neglect deficits [32,36,48].

A variety of processes presumably evolved for the purpose of directing spatial attention to relevant stimuli, involving a distributed network of cortical and subcortical brain areas all interconnected with the inferior parietal lobe [35,40]. Distinct exogenous and endogenous mechanisms of attention have been pointed out [14,40]. Exogenous mechanisms orient attention reflexively and rapidly toward important stimuli due to some elementary properties, such as sudden onset, and operate automatically without voluntary control. Endogenous mechanisms orient attention deliberately but more slowly, guided by goals and expectations, as well as more abstract properties of stimuli, such as their meaning value. A particular mechanism that is, however, not easily classified as purely exogenous or endogenous concerns the effect of perceived direction of gaze in faces. Other people’s direction of gaze constitutes a specially meaningful visual stimulus because it can reveal where they are attending, indicating locations of potential interest in the environment.
and contributing to social communication [2,30]. Recent observations in normal subjects [13,18] suggest that perceived gaze in a face can trigger shifts of visual attention in the corresponding direction. This effect shares the characteristics of reflexive exogenous orienting, as it occurs rapidly and automatically regardless of the predictive nature of gaze, even though perception of faces and eye gaze direction rely on highly specialized processes, and the attentional cueing value of gaze obviously depends on its special social meaning.

The present study investigated whether perceived gaze in faces can influence spatial attention in such an automatic manner, and modulate orienting toward the contralesional side in patients who have right parietal damage and unilateral left neglect. Parietal damage typically impairs orienting toward the contralesional side when attention is first engaged on more ipsilesional stimuli [40,41], consistent with extinction due to the competition of ipsilesional with contralesional stimuli [11,24]. Neglect patients may have difficulties in directing attention toward contralesional space both exogenously and endogenously [31]. Here, two series of experiments examined the effects of gaze cues on the perception of contralesional stimuli in standard paradigms of visual extinction (experiments 1 and 2) and speeded detection tasks (experiments 4 and 5). Effects of gaze were also compared with those produced by other symbolic stimuli such as arrows (experiments 3 and 6). The results provide support for the existence of automatic orienting mechanisms triggered by perceived gaze, which can facilitate attention to contralesional stimuli despite parietal neglect and competing ipsilesional stimuli.

In addition, the present experiments also sought to determine the perceptual basis of the mechanism by which perceived eye gaze can induce contralesional shifts of attention. In principle, such shifts might follow changes in gaze direction because it provides a signal for orienting to a given location or in a given direction, or because the lateral displacement of salient eye features induces a general bias in the spatial frame of reference upon which attention operates, be it in egocentric or allocentric coordinates [15,38,43]. Previous studies in normal subjects showing faster reaction times to peripheral targets that appear in the same rather than opposite direction of gaze do not distinguish between these possibilities. Furthermore, albeit still influencing attention in the patients, perceived gaze of faces might act in different ways on the ipsilesional and contralesional side of space.

2. Patients

Four right-handed patients with a single chronic ischemic stroke in the right hemisphere and clinical signs of visual spatial neglect were included in the study. Fig. 1 shows the extent of the lesion in each patient as reconstructed from chronic CT (SD) or MRI scans (EN, CW, JD). All patients had intact visual fields on both sides but reliable left visual extinction on bilateral simultaneous stimulation during clinical confrontation testing. SD was a 60-year-old woman, with infarction of the right middle cerebral artery (MCA) 3 years previously, dense left hemiplegia with tactile and proprioceptive sensory loss, and moderate left neglect on line bisection (mean rightward deviation 8% for 17 cm-long lines) and letter cancellation tasks (28% left-sided omissions out of 60 targets). EN was a 58-year-old man, with infarction in the right MCA 3 years previously, mild left arm paresis with decreased touch sensation, and also left neglect on line bisection (mean rightward deviation 18%) and letter cancellation tasks (35% left omissions). CW was a 66-year-old man with an infarct in the posterior and anterior watershed territory of the MCA 2 years previously, decreased dexterity and spasticity of left hand without loss of sensation, and consistent left neglect on line bisection (mean rightward deviation 35%) and letter cancellation tasks (25% left omissions). JD was a 68-year-old man with a complete MCA infarction 6 months previously, dense paralysis and sensory loss in left arm, and mild neglect on line bisection (mean rightward deviation 20%) and letter cancellation tasks (20% left omissions). All patients were alert and cooperative, without other major cognitive disturbances. They were paid for their participation and signed informed consent statements approved by the Institutional Review Board of the Martinez Department of Veterans Affairs and the University of California, Davis. Patient SD participated in all six experiments, while patients EN, CW, and JD participated only in some of them. Different experiments were administered in a given patient in separate sessions, in each case over a 6 month period during which repeated assessment of neglect showed no changes in symptoms.

3. Experiments 1–3

The first two experiments examined whether direction of gaze in faces can modulate the degree of extinction for contralesional visual stimuli. Shapes or faces were presented in the right, left, or both hemifields, with faces either looking straight ahead or toward the opposite hemifield. Two comparisons were critical on bilateral displays. The first comparison was whether an identical stimulus in the left field would be differentially extinguished when a face on the right side is looking to the left rather than straight, even though the face constitutes a similar competing stimulus in both cases. The second comparison was whether a face in the left field would be differentially extinguished when looking toward the right side rather than straight ahead, even though the competing stimulus in the right field is identical in both cases and the face on the left possibly neglected. The third experiment examined whether other meaningful stimuli (arrows) would similarly modulate contralesional extinction or not.
3.1. Methods

3.1.1. Experiment 1
Stimuli were black outline drawings of schematic faces or circular shapes (Fig. 2) presented on a white background on a computer screen. Patients sat at ∼50 cm from the screen. Each trial began with a fixation cross presented at the center of the screen (1 s), followed by face or shape stimuli (∼3° visual angle) briefly shown in either the left, right, or both hemifields (∼6° away from fixation). On both unilateral and bilateral trials, half of the faces had their eyes centered as if looking straight ahead, and the other half had their eyes deviated as if looking toward the opposite hemifield, i.e. leftward gaze for right-side faces and rightward gaze for left-side faces (Fig. 2A). There were thus three equiprobable types of unilateral trials on either side (shape, straight-gaze face, and opposite-gaze face in the right or left hemifield) and four equiprobable types of bilateral trials (left shape with either straight-gaze or opposite-gaze face on the right, and conversely, right shape with either straight-gaze or opposite-gaze face on the left). The position of shapes and faces on the screen was kept constant, with the black eye dots slightly displaced to the right or left (∼0.5°) in opposite-gaze faces as compared to straight-gaze faces. The patients were asked to report and locate the stimuli on each trial (i.e. a face, a shape, or nothing on the right and the left). Gaze direction of the faces was not relevant to the task and not explicitly pointed out in the instructions given during practice trials. Responses were typed by the examiner into the computer keyboard, and the next trial was initiated after a short interval (1.5 s). During testing, the experimenter sat opposite to the patient and checked that the central cross on the screen was correctly fixed at the beginning of each trial. Trials, where eyes deviated from fixation were noted to be discarded from subsequent analysis, and replaced by correct trials at the end of the session. Patients SD and EN were tested in two different sessions a few weeks apart (160 trials each time in both cases). The stimuli exposure duration was set during a practice phase in each patient and each session, so as to obtain a reliable rate of extinction in bilateral trials with good performance on unilateral left trials; it was then kept constant across a given session (100 and 75 ms in both SD and EN during the first and second session, respectively).

3.1.2. Experiment 2
Stimuli and procedure were exactly as in experiment 1 with the only exception that the black eye dots in faces were
A

Unilateral

+ +

B

Unilateral

+ +

Bilateral

+ +

+ +

+ +

+ +

Now always presented at the same position on the screen, while the faces’ contour was slightly displaced (~0.5°) to the right or left in opposite-gaze versus straight-gaze conditions. This modification was intended to control whether any influence of gaze on spatial attention might be caused by a subtle shift of the spatial center of mass of the visual display due to the lateral displacement of salient eye dots, rather than by the gaze direction per se (e.g. see [22,38,46]). Experiment 2 was given in a single session in patient SD (160 trials, stimuli exposure duration 100 ms) and in two separate sessions in CW (180 and 160 trials, stimuli exposure duration 200 and 150 ms, respectively).

3.1.3. Experiment 3

The general procedure was similar to experiments 1 and 2 in all respects except that faces and shapes were replaced by horizontal arrows and target circles, respectively (all ~3°). Again, there were three possible unilateral trials on either side (circle, arrow pointing rightward, arrow pointing leftward) and four possible bilateral trials (left-side circle with either rightward or leftward arrow on the right side, and conversely right-side circle with either rightward or leftward arrow on the left). In addition, circles and arrows could occupy one of two possible positions in each hemifield with equal probability, such that either the head or bar end of the arrow (respectively, the right or left edge of the circle) were aligned onto the same point on the screen (~6° from fixation), while the distance between bilateral stimuli was kept constant (Fig. 2B). Patients had to report identity (arrow, circle) and location (right, left) of stimuli. Experiment 3 was given to SD and CW in a single session (200 trials in each case, stimuli duration 150 and 200 ms, respectively).

3.2. Results

Experiments 1 and 2 yielded a similar pattern of results and were analyzed together. Most errors were misses. Recognition errors, i.e. reporting a face instead of a shape or the converse, were negligible (~1% of all trials) and did not differ between face and shape stimuli on unilateral left trials (0–0.6% versus 0–1.2%, respectively). Table 1 shows the number of stimuli missed in each condition for all three patients. All showed a marked contralesional extinction. They detected unilateral stimuli in the left visual field (LVF, 0–9% missed, mean 4.4%) practically as well as in the right visual field (RVF, 0–3% missed, mean 0.5%) but extinguished many left-side stimuli in bilateral displays (18–75%, mean 41%). Faces and shapes were equally missed on unilateral left trials (mean 5% versus 3%).

On the critical bilateral trials, the degree of contralesional extinction showed consistent differences between the four possible stimulus conditions (Fig. 3). A repeated-measure ANOVA was performed on the total miss rate in each bilateral condition for each subject in each experiment (summed across the different sessions), using face side (left versus right hemifield) and gaze direction (toward opposite hemifield versus straight-ahead) as factors. This showed significant effects of face side ($F(1, 3) = 9.99$, $P = 0.050$) and gaze direction ($F(1, 3) = 38.83$, $P = 0.008$), with a significant interaction of these two factors ($F(1, 3) = 14.75$, $P = 0.031$). Left-side faces were systematically extinguished much less than shapes in bilateral trials (32% versus 50%). More importantly, extinction was strongly modulated by gaze direction of right-side faces, but not by gaze direction of left-side faces, as reflected in the interaction of gaze and face side. Thus, in both experiments, the patients detected the presence of a shape in the contralesional LVF much more often when it was presented with a concurrent right face gazing leftward.
Table 1: Results of experiments 1 and 2 for each patient and session

<table>
<thead>
<tr>
<th>No. of stimuli missed/no. of trials</th>
<th>Experiment 1 (gaze)</th>
<th>Experiment 2 (gaze)</th>
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<tr>
<td></td>
<td>EN</td>
<td>SD</td>
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<td>Session 1</td>
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<tr>
<td>Unilateral</td>
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<td>RVF</td>
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<tr>
<td>Shape</td>
<td>0/16</td>
<td>1/16</td>
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<tr>
<td>Face gazing straight</td>
<td>0/16</td>
<td>0/16</td>
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<td>Face gazing to L</td>
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<td>LV F</td>
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<td>Shape</td>
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<tr>
<td>Face gazing straight</td>
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<td>Face gazing to R</td>
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<tr>
<td>Bilateral</td>
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<tr>
<td>Faces in LVF</td>
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<tr>
<td>RVF shape + LVF face gazing to R</td>
<td>3/16</td>
<td>4/16</td>
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<tr>
<td>RVF shape + LVF face gazing straight</td>
<td>7/16</td>
<td>4/16</td>
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<tr>
<td>Faces in RVF</td>
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<td>LVF shape + RVF face gazing to L</td>
<td>4/16</td>
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<td>LVF shape + RVF face gazing straight</td>
<td>8/16</td>
<td>7/16</td>
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*R/L, right/left; VF, visual field.

(28–50%, mean 35%) as compared with straight ahead (47–75%, mean 64%, \( F(1, 3) = 44.25, P = 0.007 \)). By contrast, left-side faces were not differentially extinguished when they were gazing rightward (17–40%, mean 29%) or straight ahead (24–44%, mean 34%, \( F(1, 3) = 1.31, P = 0.33 \)).

Inspection of individual data showed that the gaze direction of ipsilesional faces produced a consistent decrease in the number of extinguished shapes on the contralesional side in each patient and each session (see Table 1 and Fig. 3). This difference was highly significant in two cases (\( \chi^2(1) = 4.26, P = 0.038 \) for SD in experiment 1; \( \chi^2(1) = 9.95, P = 0.002 \) for CW in experiment 2), while it was nearly significant in one (\( \chi^2(1) = 3.14, P = 0.076 \) for SD in experiment 2), but less so in another one (\( \chi^2(1) = 2.4, P = 0.12 \) for EN in experiment 1). Nevertheless, all three patients clearly demonstrated the same pattern across the two experiments (see Fig. 3). Moreover, the consistency of a different proportion of extinguished LVF shapes with leftward versus straight gaze in RVF faces was highly
significant across the group as a whole ($\chi^2(1) = 26.78, P = 0.001$).

In experiment 3, with arrows and circles, both patients SD and CW correctly reported unilateral stimuli in RVF and LVF (0% and 3% misses, respectively) but again extinguished left stimuli in more than half of bilateral trials (57% arrows and 51% circles missed). However, arrow direction did not significantly influence extinction (Table 2). Even with data pooled across the patients, there was no trend indicating that the proportion of extinguished stimuli changed as a function of arrow side ($\chi^2(1) = 0.63$) or direction of right-side arrows ($\chi^2(1) = 0.05$).

In conclusion, gaze cues in faces could orient attention toward the contralesional field and alleviate extinction despite the fact they constituted competing inputs on the ipsilesional side, whereas endogenous orienting by arrow cues failed to produce similar effects. This suggests that gaze effects are unlikely to result from deliberate interpretation of gaze meaning, but rather involve specific reflexive orienting mechanisms.

4. Experiments 4-6

The following experiments employed a standard cued detection paradigm [41]. The first goal was to confirm in a different task that gaze in faces can influence spatial attention even in the presence of a contralesional deficit in patients with neglect. The second goal was to examine more precisely the nature of this influence, in particular whether gaze can direct attention toward a specific location or object on the neglected side when there is more than only one possible target. Alternatively, gaze shifts might provide a directional signal for scanning and searching within an hemifield without location specificity, or simply alter the perceived center of mass or the spatial reference frame of the scene in a way sufficient to affect the distribution of attention toward the contralesional side [38,43,46].

Moreover, while recent studies by Friesen and Kingstone [18] and Driver et al. [13] found that normal adults are faster to detect a visual target that appears at the location where a face is looking (valid cue) rather than away from it (invalid cue), there is evidence that this capability is present early in babies but limited by the boundaries of perceived or represented space [9]. Human babies as young as 2–3 months seem already equipped with an automatic mechanism that enables them to perceive changes in another person’s gaze and to look in the same general direction [26,45], but they fail to search for targets that are out of sight and fail to discriminate which of two possible locations is being fixated by the person when there are competing targets on the same side [9], suggesting that the latter capabilities depend on distinct geometric and representational spatial mechanisms that emerge only later during development.

Since patients with neglect may fail to maintain an adequate representation of the contralesional hemispace and objects therein [6,36], the present experiments examined whether perceived gaze would orient attention toward a precise location in the contralesional field when there are other possible targets on the same side, either at the same eccentricity (experiment 4) or at a closer position along the scan path from current fixation (experiment 5). Contralesional orienting should not be selective for a single location in either experiment if gaze shifts act by inducing a lateral/hemispatial bias in the coordinates of the visual reference frame or in the perceived center of mass of the display, whereas it should be selective in the former but not the latter case if gaze shifts provide directional scanning cues even without location specificity. Finally, experiment 6 examined whether orienting effects similar to those induced by perceived gaze would occur with other meaningful cues, such as an arrow pointing toward a given location in either field.
Fig. 4. Example of stimuli used in experiments 4–6. There were four possible gaze conditions in experiments 4 and 5: neutral gaze directed straight ahead, valid gaze to the same location as target, invalid gaze toward another location on the same side, or toward the opposite side. Similarly, there were four possible arrow orientation in experiment 6. Gaze or arrow direction was always irrelevant to the task and not predictive of target location.

4.1. Methods

4.1.1. Experiment 4

The test display (Fig. 4) consisted of black-outlined stimuli presented on a white background on a computer screen. Patients sat at ~50 cm from the screen. The task was to detect a peripheral target (small black square, ~0.5°) that could appear in one of four possible locations (right or left, upper or lower quadrant, ~4.5° away from fixation). Responses were made by pressing a key with the right hand as fast as possible. On each trial, a small fixation cross (~0.3°) was first presented for 700 ms, followed by a schematic drawing of a face presented centrally (~2.5° wide and 3° high) with the two eyes at the same level as the fixation cross and directed straight ahead. After a further 800 ms, the two eyes could move and look toward one of the four possible target locations (right upward, right downward, left upward, or left downward), or remain straight after a brief apparent blinking. A peripheral target then appeared after either a short (100 ms) or long (300 ms) gaze-target stimulus onset asynchrony (SOA), and remained on the screen until a response was made or 3000 ms had elapsed, whichever came first. The experiment comprised 160 target trials and 25 additional catch trials without a target (14% of all trials), given in a randomized order. There were four equiprobable gaze cue conditions in target trials, with the face looking either toward the same location as the target, toward the same side as the target but at the other adjacent location, toward the opposite side at the mirror location of the target, or in a neutral straight-ahead direction. The gaze direction had thus no reliable predictive value as to the target location (only 25% valid for the correct quadrant and 50% valid for the correct hemifield). Subjects were explicitly instructed that the central face was not relevant to the task and that the eye gaze did not predict where or when the target would appear. They were asked to respond quickly and accurately to targets, and refrain from responding on catch trials. The task was given in two sessions in neglect patients (CW, SD, JD) and in six neurologically intact right-handed subjects (3 males and 3 females, mean age 53, range 34–70).

4.1.2. Experiment 5

The task and general procedure were identical to experiment 4 with the exception of the target position, as illustrated in Fig. 4. The target was a small letter X (~0.4°) that could appear in one of four square boxes (~0.5°) displayed at two
possible eccentricities in each hemifield (inner versus outer position, 2° versus 4° away from fixation, respectively), all aligned with the lower part of the face. On each trial, the four boxes were presented with the central face (800 ms), preceded by a fixation cross (700 ms), and followed by the two eyes moving so as to look toward one of the four possible target locations (left outward, left inward, right outward, or right inward), or remaining straight-ahead after a brief blinking. The targets were presented after a short or long SOA (100 or 300 ms) in a randomized order (160 trials), remaining on the screen until a response was made or 3000 ms had elapsed, and were mixed with 25 additional catch trials without a target (14% of all trials). Again, there were four equiprobable gaze cue conditions in target trials, with the face looking either toward the same location as the target, toward the same side as the target but at the other location, toward the opposite side at the mirror location of the target, or in a neutral straight-ahead direction. As previously, gaze direction did not predict the target location (50% valid for the correct hemifield and 25% valid for the correct box), and subjects were explicitly instructed that the face and eye gaze were not relevant to the task. The same three patients with left spatial neglect (CW, SD, JD) and six normal subjects were tested.

4.1.3. Experiment 6

The task and procedure were essentially similar to experiment 4 except that the central face was replaced by an arrow appearing across a central circle, like in a clock or compass (Fig. 4). On each trial, a fixation cross was first presented at the center of an empty circle for 700 ms, replaced by a vertical arrow (∼2°) pointing upward for 800 ms, which then changed into an arrow pointing to one of four possible directions (right upward, right downward, left upward, or left downward) or a vertical arrow pointing downward (neutral cue). After a short (100 ms) or long (300 ms) interval, a small square target appeared in one of the four quadrant locations (∼5° away from fixation) and remained on the screen until a response was made, or 3000 ms had elapsed. Subjects had to press a key as fast as possible after target appearance. On an equal number of trials, arrow cues pointed either toward the same location as the target, toward the same side but at the adjacent location, toward the opposite side at the mirror location, or in a neutral downward direction. As in experiments with gaze cues, subjects were told that arrow direction was not predictive of target location (25% validity). There were 160 target trials and 25 catch trials without a target (14%) in random order. The three neglect patients (CW, SD, and JD) were tested in a single session.

4.2. Results

Mean reaction times (RTs) were calculated for each subject and target position in each condition after outliers (above and below 2 SD from the mean) were removed (≤2.7% of data in both experiments). Anticipation (RT < 100 ms) and incorrect responses on catch trials were rare (≤1.1% of all trials in normal cases and patients) and excluded from further analysis.

4.2.1. Experiment 4

Performance of normal subjects revealed that gaze cues can orient attention toward a specific location (Fig. 5). Mean RTs were submitted to a repeated-measure ANOVA with gaze direction (same location, same field, opposite field, or straight), SOA (short or long), target position (upper or lower), and field (left or right) as within-subject factors. This showed strong effects of gaze direction (F(3, 15) = 60.85, P < 0.0001) and SOA (F(1, 5) = 248, P < 0.0001), but no effect of target position or field (all F = 1.28). There was no interaction except between SOA and gaze cues (F(3, 15) = 9.87, P = 0.008), due to a significant difference in RTs between neutral gaze and opposite or same-side gaze at long but not short SOA. Across all conditions, RTs were faster after long SOA (mean 328 ms) than after short SOA (384 ms).

Planned comparisons between gaze conditions showed that detection was always faster when the face looked to the same location as the target (mean 328 ms) rather than straight (396 ms; paired t-test across subjects, t(5) = 10.2, P < 0.05) or to another location on the same side (343 ms; t(5) = 3.07, P < 0.05). The latter was true at both short and long SOA, as confirmed by a separate ANOVA showing an effect of gaze validity (same location versus same side, F(1, 5) = 9.47, P = 0.027) and SOA (F(1, 5) = 134, P < 0.001) but no interaction (F(1, 5) = 0.58, P = 0.48). In addition, invalid gaze to another location in opposite or same field did not differ (343 ms versus 347 ms; t(5) = 2.08, P > 0.05), suggesting similar shifts of attention between and within fields. Finally, straight gaze produced the slowest mean RTs (396 ms) in comparison to other averted gaze conditions; the same finding was reported by Friesen and Kingstone [18], and might reflect a warning effect due to sudden eye motion, or attention being captured at fixation by straight gaze.

In this task, the three patients exhibited similar influences of gaze on both sides (Fig. 5). Target detection was faster in ipsilesional than contralesional field (mean 431 ms versus 450 ms), and faster with longer than shorter SOA in both fields (456 ms versus 485 ms). A repeated-measure ANOVA combining mean RTs from each patient as above showed main effects of field (F(1, 2) = 23.2, P = 0.037), SOA (F(1, 2) = 19.9, P = 0.046), and gaze direction (F(3, 6) = 5.34, P < 0.039). There was no effect of target position (upper or lower quadrant, F(1, 2) = 0.99) and no interaction (all F ≤ 1.68). The critical planned comparisons between gaze conditions showed that target detection was facilitated in both fields when eyes were directed toward the same location (RVF: 399 ms; LVF: 473 ms) compared with straight gaze (RVF: 445 ms, paired t-test across SOAs, t(5) = 3.13, P < 0.05; LVF: 536 ms, t(5) = 2.91, P < 0.05), and also compared with gaze toward another location on the same side (RVF 431 ms, t(5) =
Fig. 5. Results of experiments 4 (upper row) and 5 (lower row). Mean reaction times (±S.E.) are shown for normal controls (left graphs) and three neglect patients (CW, JD, and SD; right graphs), as a function of gaze direction in the central face (i.e. same location as target), another location on the same side, opposite side, or straight ahead. In controls, responses were slower at short than long gaze-target asynchrony (SOA 100 ms versus 300 ms), and faster with gaze directed to the same side or the same location as targets. In patients, responses were slower to contralesional (L VF) than ipsilesional (RVF) targets, but still facilitated in the direction of gaze cues; their RTs were also faster with same-location rather than same-side gaze on both sides in experiment 4, but not in experiment 5 (see Fig. 6).

By contrast, target detection was not faster with gaze toward another location on the same side as compared to neutral gaze in either L VF or RVF (t(5) = 1.86, P > 0.05). This suggests that gaze direction did not merely induce a general hemispatial bias, but rather cued specific quadrant locations, both in ipsilesional and contralesional space.

In patients, invalid gaze toward the opposite side slowed detection more than invalid gaze toward another location on the same side for targets in either hemifield (Fig. 5), but this additional delay for between-field shifts was significant only for L VF targets (535 ms versus 497 ms, t(5) = 2.46, P = 0.05). By contrast, target detection was not faster with gaze toward another location on the same side as compared to neutral gaze in either L VF or RVF (t(5) = 1.86, P > 0.05). This suggests that gaze direction did not merely induce a general hemispatial bias, but rather cued specific quadrant locations, both in ipsilesional and contralesional space.

4.2.2. Experiment 5

In normal subjects, gaze again cued attention toward a specific target location, with little difference between inner and outer positions (Fig. 5). A repeated-measure ANOVA on mean detection RTs indicated main effects of gaze direction (same location, same side, opposite side, or straight; F(3, 15) = 21.6, P < 0.001) and SOA (short or long; F(1, 5) = 6.3, P = 0.05), no effect of field (left or right; F(1, 5) = 2.2, P = 0.19), and only a marginal effect of target position (inner or outer; F(1, 5) = 4.2, P = 0.097). RTs were faster after long (mean 368 ms) than short SOA (405 ms), and slightly faster for inner (382 ms) than outer (391 ms) targets. There was no interaction except for gaze and SOA (F(3, 15) = 8.8, P = 0.001).
Planned comparisons between gaze conditions revealed that same-location gaze speeded target detection compared with straight gaze at both short SOA (366 ms versus 417 ms, $t(5) = 2.5, P = 0.05$) and long SOA (341 ms versus 397 ms, $t(5) = 17.5, P < 0.001$), and also compared with gaze toward an adjacent location on the same side at long SOA (366 ms, $t(5) = 5.6, P < 0.005$) but not short SOA (392 ms, $t(5) = 0.66$). On the other hand, opposite gaze slowed detection more than invalid gaze to the same side at short SOA (423 ms, $t(5) = 6.2, P < 0.05$) but not long SOA (367 ms, $t(5) = 0.06$). Neutral gaze were again slower than other conditions except for opposite gaze at short SOA (Fig. 5).

As in the previous experiment, the three patients were slower for detecting contralesional targets (mean 956 ms) than ipsilesional targets (524 ms), but now gaze effects differed between fields and target locations (Fig. 5). A repeated-measure ANOVA was performed on mean RTs from each patient with the same within-subject factors as above, including field, gaze direction, SOA, and target position. This showed main effects of field ($F(1, 2) = 36.8, P = 0.026$) and gaze ($F(3, 6) = 5.7, P = 0.035$), but not of SOA ($F(1, 2) = 3.4, P = 0.21$) and position ($F(1, 2) = 2.0, P = 0.29$). There was a marginal interaction between position and field ($F(1, 2) = 13.7, P = 0.066$) due to much slower responses to outer than inner targets in the LVF (1139 ms versus 773 ms), in comparison with the RVF (540 ms versus 509 ms). Most importantly, unlike in the previous experiment, the effect of gaze interacted with field ($F(3, 6) = 5.4, P = 0.038$), and there was a triple interaction of gaze with side and position ($F(3, 6) = 7.5, P = 0.019$). The source of these interactions was revealed by the following comparisons between critical gaze conditions.

In the RVF, same-location gaze facilitated target detection (mean 474 ms) as compared to gaze toward an adjacent location on the same side (Fig. 5), irrespective of SOA and position (560 ms; paired t-test $t(11) = 2.67, P < 0.05$), but there was no such effect in the LVF (or even a converse trend; 761 ms versus 712 ms, respectively; $t(11) = 1.0, P > 0.05$). However, detection of LVF targets was facilitated by same-side gaze as compared to neutral straight gaze (712 ms versus 978 ms, $t(11) = 2.2, P = 0.05$), suggesting that leftward gaze shifted attention toward contralesional space but did not cue a specific location on this side in this experiment.

In addition, detection was slower after invalid gaze toward the opposite side than toward the same side for LVF targets (1372 ms versus 712 ms) but not for RVF targets (541 ms versus 560 ms). Further, the interaction of gaze and side with target position reflected the fact that this slowing due to opposite gaze was more marked for LVF targets at the outer location (1775 ms) than at the inner location (968 ms); and remarkably, it also reflected the fact that detection of RVF targets was slower at the inner location (589 ms) than at the outer location (531 ms) when gaze was invalidly directed toward the adjacent location on the same side, whereas it was faster at the inner than outer location in all other RVF conditions (including same-location gaze: 453 ms versus 495 ms, respectively), as well as in all other LVF conditions (Fig. 6). This finding suggests a difficulty disengaging attention leftward toward inner targets within the ipsilesional RVF when first cued to a specific outer location. This paradoxical effect in the patients was confirmed by an analysis restricted to responses for RVF targets, using group (patients versus controls) as a between-subject factor and gaze (same location versus same side), position (inner versus outer), and SOA (short versus long) as within-subject factors. This showed main effects of group ($F(1, 7) = 23.5, P = 0.002$) and gaze ($F(1, 7) = 8.3, P = 0.002$), but no effect of position ($F(1, 7) = 0.01$) and SOA ($F(1, 7) = 0.40$), with a significant interaction of gaze × position ($F(1, 7) = 5.9, P = 0.046$) and gaze × position × group ($F(1, 7) = 7.6, P = 0.028$).

Finally, the repeated-measure ANOVA of all conditions in the patients also revealed an interaction of gaze and SOA ($F(3, 6) = 5.5, P = 0.037$), together with triple interactions of gaze × SOA × side ($F(3, 6) = 7.3, P = 0.02$),
and gaze × SOA × position (F(3, 6) = 4.9, P = 0.048). This reflected the fact that RTs were slower at shorter than longer SOA with neutral gaze especially for outer targets, on both sides (LVF: 1403 ms versus 498 ms; RVF: 648 ms versus 498 ms), and for inner targets on the contralateral side (LVF: 987 ms versus 734 ms; RVF: 474 ms versus 473 ms). Other interactions were not significant (F = 2.1).

In sum, in the patients, gaze direction could effectively cue attention to specific horizontal locations in ipsilesional space, with a subsequent difficulty re-orienting leftward (to the inner position) after invalid cueing of the more peripheral (outer) position on the same side. However, gaze oriented attention toward the contralateral space without location-specific benefits, and cued only the inner but not the outer position. This therefore contrasted with the quadrant-specific benefits found in the previous experiment.

4.2.3. Experiment 6

In contrast to experiments 4 and 5 with gaze cues, no reliable pattern was obtained in experiment 6 with arrows. Mean RTs from the three patients were submitted to a repeated-measure ANOVA as above. There was a significant effect of field due to slower RTs for left than right targets (mean 579 ms versus 478 ms, F(1, 2) = 17.8, P = 0.05), and nearly significant effect of SOA due to slower RTs at short than long SOA (515 ms versus 541 ms, F(1, 2) = 13.6, P = 0.06), but no effect of target position (upper or lower position, F(1, 2) = 1.31), and most importantly, no effect of arrow direction (same location as target, same side as target, opposite side, or neutral downward, F(3, 6) = 0.4).

Thus, arrows pointing toward the same location as targets did not facilitate detection in either hemifield, as compared to arrows pointing toward another location or to neutral arrows pointing downward (RVF: 467 ms versus 484 ms versus 491 ms, respectively; LVF: 566 ms versus 550 ms versus 575 ms, respectively). However, arrow direction interacted with field and SOA (F(3, 6) = 14.5, P = 0.004) reflecting the fact that RTs were particularly slowed for left-side targets when arrows pointed toward the opposite side at long SOA (589 ms versus 521 ms for neutral arrows, paired t-test t(5) = 4.7, P < 0.01). There was no other significant interaction. These results suggest some degree of endogenous orienting produced by the rightward arrows, delaying detection in contralateral LVF, but no consistent effect of the leftward arrows.

5. Discussion

Faces and perceived direction of gaze influenced spatial attention in parietal-damaged patients across different tasks. This influence still operated towards stimuli on the contrale- sional side despite unilateral neglect and extinction, partly overcoming the patients’ pathological spatial bias. By contrast, symbolic arrow cues had only minimal or no effect. Although arrow cues differ from gaze cues in a number of ways, the lack of effect with arrows suggests that gaze effects did not simply result from spontaneous endogenous orient- ing strategy. These results support the existence of special- ized mechanisms reflexively shifting attention in response to perceived gaze, and suggest they are at least in part distinct from those affected by parietal injury.

In experiments 1 and 2, contralesional extinction was strongly modulated by the nature of stimuli. First, faces were less extinguished than shapes, irrespective of their gaze di- rection. This replicates similar recent findings in patients [51,55], and accords with the view that contralesional field information may be processed in ventral occipitotemporal cortex independently from spatial attention, up to the level where recognition processes can extract facial traits and dis- criminate faces from other stimuli [51,52]. Moreover, faces may have a special advantage in capturing attention even in normal subjects, reflecting their particular familiarity and saliency, as well as their special biological and social value [33,58].

Secondly, a novel finding was that extinction was strongly influenced by gaze direction in ipsilesional faces. The same shapes at the same location in LVF were missed when a current right-side face looked straight ahead, but detected when the face looked to the left. This occurred even though gaze direction was not relevant to the task, and con- tralesional stimuli were identical. This effect cannot be explained by a shift in the perceived center of mass of the display due to displacing the eye dots (in experiment 1), since it was unchanged when gaze shifts were created by displacing the face contour to the ipsilesional side, with the eyes remaining at the same location on the screen (experiment 2). On one hand, this shows that perceived gaze can trigger strong and automatic orient- ing of attention, even when it is irrelevant to the task [13,18]. On the other hand, it supports the view that extinction en- tails a problem in orienting attention to contralesional stim- uli [11,24], rather than a mere degradation of sensory inputs [4,48], because the same contralesional stimuli were extin- guished or not depending on the gaze of an ipsilesional face.

Thirdly, experiments 1 and 2 showed that gaze of con- tralesional faces had no effect, although it would have been in a position to bias attention in the ipsilesional direction and, thus possibly exacerbate extinction. Alternatively, gaze shifts (both in contralesional and ipsilesional faces) could have influenced extinction by affording some sort of per- ceptual grouping between the face and the opposite shape (e.g. [53,56]), in which case rightward gaze in contrales- sional faces would have reduced extinction. This asymmet- ric effect of gaze suggests it cannot be explained by visual grouping. Moreover, this indicates that gaze information is not extracted by “preattentive” processes which could po- tentially still operate in the left hemifield (e.g. [12,29]). By contrast, perceptual organization into a face gestalt [47,51]
and discrimination of emotional facial traits [54,58] can still arise in the left field. Therefore, although gaze can affect attentional orienting in an automatic manner, this seems to occur only when the face receives sufficient attention. This does not support a common belief according to which other people’s direction of gaze can be detected unconsciously or without attention (e.g. [7]).

These results also complement recent findings in split-brain patients [29], showing that attentional effects due to gaze may depend on cortical circuits lateralized in the hemisphere dominant for face processing and may predominantly operate within one hemifield. Here, left neglect patients showed that gaze direction of faces in RVF facilitated detection of stimuli in LVF, suggesting a modulation of visual inputs operating across hemifields when callosal connections are intact. By contrast, faces presented in the LVF, and thus projecting to the right hemisphere, had no significant effect on visual detection within the same LVF. Because it seems unlikely that all three of the present patients had atypical hemispheric dominance for face processing, the lack of effect due to LVF faces in this situation might reflect damage to right intra-hemispheric connections between intact face and gaze processing areas (in temporal cortex) and other areas specialized for shifting spatial attention (in right posterior parietal cortex) [29], or the need for facial gaze cues to be processed with attention in order to elicit subsequent orienting.

Using a different paradigm, experiments 4 and 5 further confirmed that perceived gaze can orient attention to contralesional space in neglect. Although the patients’ responses were slower on the left, peripheral targets in either field were detected faster when a central irrelevant face looked in the direction of the target, and slower when the face looked in the opposite direction. Also, in both experiments, opposite gaze slowed detection of left more than right targets, indicating a disproportionate deficit in disengaging attention contralesionally when it was first oriented to the ipsilesional side [41]. This leftward disengagement cost arose even within the intact right field, with delayed responses to inner right targets when the face looked to another more eccentric location on the same side. Again, these effects occurred even though the face and gaze cues were irrelevant to the task and nonpredictive as to where targets would appear. Moreover, they emerged rapidly, as early as 100 ms after gaze cue onset in both hemifields, consistent with a reflexive mechanism [14,40].

Reflexive orienting to perceived gaze was previously found in normal adults [13,18] and babies as young as three months [26]. The present results extend these findings by demonstrating that similar effects may persist despite a pathological bias in attention after parietal damage. Further, they suggest that different component mechanisms may operate on the two side of space in the patients. Experiments 4 and 5 together show that attentional shifts following gaze do not simply result from a global hemispatial bias in the reference frame dictated by the task, in egocentric or allocentric coordinates [15,38], or from a change in the center of mass of the display due to displacing salient facial elements [38,46]. In principle, both perceptual mechanisms might account for faster orienting to targets on the side of gaze shifts [38,43]. However, the current experiments show that in normal subjects, and in the right field of patients, gaze signals can specify not only the general direction but also a precise location in space where attention is selectively allocated, even when there is another competing target location on the same side, closer to fixation along the scanning path. By contrast, in the left field of patients, gaze cues oriented attention toward distinct spatial quadrants (experiment 4), but did not afford the selection of a specific peripheral location when there was another possible target in a more ipsilesional location (experiment 5).

Gaze to the contralesional side thus appeared to act mainly as a directional signal for reflexive scanning and searching in the corresponding direction without coding for a specific horizontal location. This may reflect an inability to maintain a stable representation of locations and objects along the horizontal axis within contralesional hemispace [6,36,53], consistent with a crucial role of parietal cortex in coding the spatial location of relevant stimuli [1,21].

Gaze-following is a fundamental visuomotor behavior that has its roots in early development and perhaps pre-wired neural mechanisms [3,49]. People are extremely sensitive to eye gaze direction [50], which constitutes a major social signal [2,30]. Human babies can detect the presence of eye-like stimuli early after birth [27,34], perceive gaze directed toward or away from them at 2-3 months of age [23,49], and follow the direction of their mother’s gaze at 4-6 months [9,37,45]. Even, 10-week-old babies covertly orient to peripheral targets in response to perceived gaze shifts [26], just like adults do [13,18]. Gaze following in children may contribute to joint attention and learning of cognitive skills [37], and to the development of a “theory of mind” about intentions of other people [3]. However, the ability to discriminate which location is gazed at when there is more than one possible target on the same side may require additional cognitive mechanisms for representing space and geometric relationships, not fully developed until age 4 or 5 years [9,17]. Thus, children younger than 12 months orient in the direction of gaze (right or left) but fail to search beyond the field of immediate view (e.g. for objects hidden or behind them), whereas at 18 months they can orient to an unseen stimulus but invariably rest at the first interesting object encountered along the scanning path, even if it is not the one fixated [9]. By analogy, in neglect patients, experiments 4 and 5 suggest that gaze cues might influence attention toward the contralesional space through directional scanning mechanisms similar to those seen in early developmental stages, allowing reflexive shifts in a given direction but not to a single peripheral location when there is another competing location along the scan path. Even in normal subjects, in experiment 5, same-location gaze benefited target detection more than same-side gaze only at longer SOA, not at short
SOA, consistent with the fast and automatic effects of gaze being primarily directional and location-specific effects involving a later stage.

Data from neuropsychology [10,60], functional neuroimaging [25,28,42,59], and monkey neurophysiology [8,39] suggest that gaze signals are processed in the superior temporal sulcus and amygdala. These areas are reciprocally connected with cingulate and parietal cortex [39], and thus in a position to influence cortical networks of spatial attention [35]. Recent fMRI studies found that eye movement in faces activate the intraparietal sulcus [25,42,59], implicated in shifts of attention [20,35]. However, the right parietal cortex was destroyed in all patients here, resulting in left neglect and extinction. This suggests that attentional effects of gaze cues on LVF stimuli in these patients could not rely only on lateralized right-hemispheric circuits between intact face processing areas of temporal cortex and parietal cortex itself [29]. Note that besides parietal cortex, gaze signals activate the amygdala [28] and lateral occipitotemporal junction [42,57,59]. The latter areas are implicated in ocular pursuit and spatial shifts of attention [20,44], they were spared in the patients (Fig. 1) and might directly interact with face and gaze processing in inferior temporal lobe and/or amygdala to shift attention in the contralateral direction, even when parietal damage precludes other spatially-based mechanisms of selection. Interestingly, visual pathways from striate cortex to the occipitotemporal junction mature before other ventral and dorsal pathways in infants [27], possibly underlying their early development of gaze following [49]. Alternatively, reflexive orienting of attention to perceived gaze might involve subcortical pathways in the superior colliculus, but this is unlikely because if these effects are (i) not larger for saccadic than manual responses [19], (ii) not replaced by inhibition of return with longer SOAs [13], (iii) not influenced by offsetting the face at fixation, which should enhance reflexive collicular activity [19].

Note finally that in experiments 4 and 5, in normal subjects, straight gaze in faces slowed responses to peripheral targets, even more than gaze directed to an invalid location. Friesen and Kingstone [18] reported a similar finding and suggested, Harris Ingle for anatomical reconstruction of the lesions. This work was supported by grants from the Swiss National Science Foundation (81-GE-500080), US Public Health Service (R01 MH41544), and the Human Frontier Science Program.

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References

[38] Shanes JS, Jacobs DH, Heilman KM. The influence of center of mass effect on the distribution of spatial attention in the vertical and horizontal dimension. Brain & Cognition 1997;34:293–300.