

Object-Based Inhibition of Return in Patients With Posterior Parietal Damage

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Recent evidence has shown that inhibition of return, IOR, is impaired in patients with parietal damage with or without clinical signs of neglect (Bartolomeo, Sieroff, Decaix, & Chokron, 2001; Vivas, Humphreys, & Fuentes, 2003, respectively). In addition to environment-based IOR, Tipper et al. (1991) showed that IOR could be also associated with dynamic, object-based representations. In our study, we examined four patients with unilateral lesions to the parietal lobe, and a group of healthy controls, in an IOR procedure with moving objects where a pre-cued object could move, clockwise or counter-clockwise, 90° in polar coordinates. The group of control participants showed a small but significant object-based IOR effect. In contrast, the patients showed an object-based IOR effect when the objects moved from the contralesional field toward the ipsilesional field, whereas there was no IOR effect when they moved from the ipsilesional to the contralesional field. These findings are discussed in terms of the role of the parietal cortex in implementing attentional biases in both environment-based (Vivas et al., 2003) and object-based frames of reference.

Keywords: inhibition, parietal lobe, saliency map, visuospatial attention

Psychophysical and neuropsychological evidence suggests that visual attention can be directed to particular locations in a spatial map (LaBerge, 1983; Posner, 1980), as well as to perceptual groups (Baylis & Driver, 1993; Kahneman & Treisman, 1984; Duncan, 1984). In line with this, inhibitory biases in visuospatial attention (inhibition of return, Posner & Cohen, 1984) seem to operate in both environment-based and object-based frames of reference. The inhibitory bias known as inhibition of return (IOR) was first reported by Posner and Cohen (1984). These authors demonstrated that response times (RTs) were delayed to target stimuli that appeared in the locations of boxes that had been previously illuminated, compared with RTs to targets appearing in an uncued box. However, in such studies attention may be biased either away from objects (the boxes) or the locations of the luminance cue, and it is difficult to disentangle the contribution(s) of the cued location or the cued object to the inhibitory effect. In a later study, Tipper et al. (1991) showed that if the task changed,

and participants had to respond to targets that appeared inside boxes that moved across the field, then the inhibition moved with the object. Furthermore, the results of their study showed that two different effects contribute to the total magnitude of IOR, because the location-based effect remained at the cued location even if the boxes moved. The second object-based effect was evidenced as slowed RTs to stimuli that appeared inside the previously cued object, relative to stimuli appearing in an uncued object that had moved into a new location (e.g., after the peripheral spatial cue the boxes rotated 90° in polar coordinates). Tipper, Weaver, Jerreat, and Burak (1994) concluded that two different types of representations may underlie IOR, one based on the location (a region of the space) and another based on the object itself. These two different forms of IOR might aid visual search in different conditions (e.g., looking for a stationary object and looking for a friend in the airport, respectively).

IOR with static displays is a robust phenomenon that can be generalized to different types of tasks (e.g., detection and discrimination) and responses (e.g., manual response and eye movement latencies; see Klein, 2000, for a review). However, there has been some debate over dynamic, object-based IOR. Although several studies have replicated the IOR effect with displays that circle around fixation (Abrams & Dobkin, 1994; Tipper et al., 1994; McCrae & Abrams, 2001; Weaver, Lupiañez, & Watson, 1998) and in displays with translational motion (Ro & Rafal, 1999), there has also been a failure to replicate IOR with dynamic displays (see Müller and von Mühlénen, 1996). Experimental factors such as the relative saliency of the central cue (the fixation point), which can draw attention away from the cued object (Ro & Rafal, 1999), or practice effects (Müller & von Mühlénen, 1996), might account for the contrasting results. Moreover, several studies have reported

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IOR with dynamic displays in which trials with eye movements are discarded (Abrams & Dobkin, 1994; Tipper et al., 1994), suggesting that object-based IOR is not an eye-movement artifact.

Particularly relevant to our study, Tipper and coworkers proposed that contrasting forms of inhibition might be mediated by different cortical systems (Tipper et al., 1994, 1997). Early research on location-based IOR (Posner, Rafal, Choate, & Vaughan, 1985; Sapir, Soreker, Berger, & Henik, 1999) suggested that location-based IOR was associated with relatively primitive mid-brain areas such as the superior colliculus (SC). In contrast, Tipper et al. (1994, 1997) proposed that object-based IOR might involve a more sophisticated cortical system capable of tracking moving objects. In their study, the authors examined location-based and object-based IOR in a group of patients with split-brain surgery. Although the patients exhibited intact location-based IOR, they showed object-based IOR only when the object moved within the same visual hemifield. In contrast, when the object moved across visual hemifields, the split-brain patients showed object-based facilitation instead of inhibition. This suggests that object-based IOR requires that information be coordinated across the cerebral hemispheres, although it does not link object-based IOR to any particular site within the cortex.

In agreement with the idea of different cortical sites subserving the two forms of IOR, studies with older adults have showed a dissociation between the location-centered and object-centered IOR effects (McCrae & Abrams, 2001). Thus, McCrae and Abrams (2001) reported intact location-based and object-based IOR in a group of young adults, using a similar procedure to the one employed by Tipper et al. (1991). Also, in line with previous studies (Faust & Balota, 1997; Langley, Fuentes, Overmier, Bastin de Jong, & Prod'Homme, 2001), McCrae and Abrams found that location-based IOR was not disrupted in older adults. However, the older adults showed object-based facilitation instead of inhibition with the dynamic display. This finding suggests a differential pattern of breakdown of these two inhibitory effects with aging and may lead to the conclusion that object-based IOR is associated with cortical areas more susceptible to the effects of aging.

Although the conclusion by Tipper and colleagues that cortical areas may subserve object-based IOR awaits corroboration, the claim that location-based IOR is subserved by subcortical mechanisms concerned with oculomotor control has been challenged by more recent studies. For instance, studies using functional neuroimaging have reported that IOR is associated with significant activation of cortical areas including the frontal eye fields, the superior parietal cortex, and anterior motor areas. In contrast, activation is not necessarily found in the superior colliculus (Lepsien & Pollmann, 2002; Rosen et al., 1999). These data have been further supported by recent neuropsychological studies. For instance, Sapir, Hayes, Henik, Dazinger, and Rafal (2004) found a deficit in environmental encoding of IOR for both visual fields in patients with damage to the right intraparietal sulcus, using a double-step saccade paradigm, and concluded that the parietal lobe may actually be responsible for the encoding of the inhibitory signal in a location-centered frame of reference. Other research has reported a disruption of location-based IOR in patients with inferior parietal lesions (Bartolomeo, Chokron, & Sieroff, 1999; Bartolomeo et al., 2001; Vivas et al., 2003). In these studies, such patients failed to exhibit IOR for ipsilesional items (Vivas et al.,

2003), even when the stimuli were displayed vertically, and, on invalid cue trials, a target appeared in the same ipsilesional hemifield as the cue so that there was no need for to shift attention horizontally across the visual field (Vivas, Humphreys, & Fuentes, 2006). This last result suggests that the problem is not merely one of spatial disengagement of attention from the ipsilesional field in order to orient to stimuli appearing in the contralesional field, because the problem would then arise only when the cue is in the ipsilesional field and the target is in the contralesional field (cf. Posner & Cohen, 1984).

To explain these findings, we proposed that the parietal lobe represents the salience of stimuli in the visual field (Colby & Goldberg, 1999; Gottlieb, Kusunoki, & Goldberg, 1998). Electrophysiological studies with monkeys have shown that the activity of neurons in the lateral intraparietal cortex encodes the salience of a stimulus at a given location, regardless of whether salience is defined as an intrinsic attribute of the stimulus (i.e., an abrupt onset) or determined by the relevance of the stimulus for the task at hand. This salience map may then guide the selection of targets for potential saccades along with covert shifts of spatial attention (Colby & Goldberg, 1999; Gottlieb et al., 1998). The idea that a salience map is used to guide attention has been proposed repeatedly in the literature, and salience maps have been incorporated into models of visual search (Koch & Ullman, 1985; Itti & Koch, 2000, 2001; Wolfe, 1994). Koch and Ullman (1985) proposed that the saliency of objects in the visual environment is explicitly encoded in a two-dimensional map, and that attention is then deployed to locations in this map in a sequential, descending order of salience. In later versions of this model, the authors included an inhibitory feedback to the salience map, to prevent the "winner" (the most salient location) from being continuously selected. This inhibitory component can be linked to the phenomenon of IOR (Itti & Koch, 2000, 2001; see also Heinke & Humphreys, 2003, for a similar approach). We (Vivas et al., 2003; 2006) proposed that parietal damage may selectively affect the saliency map so that there is a relative imbalance in the saliency of stimuli in the ipsilesional and contralesional fields (see Heinke & Humphreys, 2003, for an explicit simulation). That is, unilateral lesions weaken the input from contralesional stimuli into the saliency map, rendering contralesional stimuli less competitive and biasing competition to favor stimuli on the ipsilesional side. As a consequence, stimuli falling at ipsilesional locations may have a higher "attentional weighting" (and greater salience) than those falling at contralesional locations. This may be akin to healthy adults giving greater attentional weight to stimuli that are larger or brighter than their competitors (Heinke & Humphreys, 2003). For the patients, we propose that the increased salience of ipsilesional signals may be sufficient to overrule any IOR. This means that, in patients with unilateral lesions to the parietal lobe, the focus of attention may become "stuck" in an ipsilesional location.

The parietal lobe may also be a suitable candidate for object-based IOR in dynamic displays because converging evidence from neuropsychological and brain imaging studies indicate that the parietal lobe receives connections from motion-processing regions in the human temporal cortex (hMT/V5+) (Battelli et al., 2001; Claeys, Lindsey, Schutter & Orban, 2003; Zeki et al., 1991), and the parietal lobe is strongly implicated in tracking moving objects (Culham et al., 1998; Culham, Cavanagh, & Kanwisher, 2001). If

this is the case, then both forms of IOR, location- and object-based, may recruit similar (overlapping) neural networks, including the posterior parietal lobe.

In our study, we investigated whether a bias in the relative salience of ipsilesional signals, because of spatially asymmetric lesions to the parietal lobe, may affect object-based IOR. Also, we tested the hypothesis that both forms of IOR, location-based and object-based, may be mediated by a similar network of brain areas including the parietal cortex. To test these hypotheses, we examined a group of patients with unilateral lesions to the parietal lobe on a typical object-based IOR paradigm. Patients were cued with a brief illumination of a box in either their ipsilesional or contralesional field. The boxes then moved and halted when positioned in the vertical meridian, after which the target could appear in either the cued or the uncued box. This manipulation separates the field where a cued is first presented from the final presentation of the target, which falls in the vertical meridian. If there is impairment in applying object-based IOR in the contralesional field, then there should be no IOR to targets that fall in locations that were originally cued in the contralesional field and have to be tracked through that field until they reach the vertical meridian. However, a different prediction can be made based on the idea that unilateral parietal lesions lead to an imbalanced competition of objects/locations for selective attention. That is, if the input of contralesional stimuli to the saliency map is weakened by the lesion, then ipsilesional stimuli would have by default a greater overall salience. If this is the case, then the patients may manifest reduced IOR when stimuli were initially cued in their ipsilesional field (and so are highly salient), even when these items move toward the contralesional field.

Method

Participants

Five healthy adults participated in the experiment. Their age ranged from 50 to 67 years, with a mean of 55 years. They all had normal or corrected-to-normal vision. We examined four patients, all with unilateral lesions affecting the inferior parietal lobe (MH, PF, RH, MP), three of them in the left hemisphere (MH, PF, RH) and one with a right hemisphere lesion (MP). All the patients showed visual extinction, except MP who manifested unilateral neglect on standard tests requiring spatial scanning of attention (e.g., star or line cancellation). Clinical details of the patients are presented in Table 1, and transcriptions of their lesions are shown in Figure 1.

Stimuli

The experimental task was created with use of MEL (Micro Experimental Laboratory; Schneider, 1988). The target consisted

of a small red square that could appear inside of one of the peripheral boxes (up and down). Participants had to press the space bar as soon as they saw the target stimulus.

Procedure

A trial began with a fixation cross in the center of the screen. The fixation point remained on the screen until the experimenter judged that the patient was looking at the fixation and ready to continue. Then three squares appeared on the screen, one containing the fixation cross, and one of each side equidistant from the fixation (see Figure 2). Each outer square was positioned 20° below and above the central square in the initial display, which remained in the screen for 500 ms. Then apparent motion of the outer squares was created by presenting a series of frames, in which the distance between adjacent positions was 10° (in polar coordinates). Thus, 11 frames were presented to create a clockwise or counterclockwise motion of 90° in polar coordinates. In the initial display, the left square in the clockwise motion condition and the right square in the counterclockwise condition fell 10° below the horizontal line, with the opposite outer square also 10° above the horizontal line. This remained for 66 ms. The squares moved for 66 ms to an intermediate position before being aligned with the horizontal meridian in a third frame. One of the outer squares was then thickened for 100 ms (the peripheral cue). The stimuli remained static and uncued for an additional 200 ms, when the central cue was subsequently presented for 100 ms while the outer squares continued to move smoothly in a clockwise or counterclockwise direction around the central square. Finally, after 662 ms from the onset of the peripheral cue, a target appeared inside one of the outer squares, when they were aligned vertically (90° in polar coordinates). The target remained in the screen until the participant responded by pressing the space bar. On absent trials, the participants were instructed not to respond.

Patients and control participants run two practice blocks, one for each direction of motion condition (clockwise and counterclockwise), each with 24 trials followed by four experimental blocks of 50 trials, two experimental blocks for each direction of motion condition. In each experimental block, the target was present on 40 (80%) trials, and it was absent on 10 (20%) trials. On half of the present trials (20), the target appeared in the upper outer square, and in the lower outer square on the remaining trials. Also, for each field, the target appeared in the previously cued square on half of the trials (10), and on the remaining trials it appeared in the uncued square. The order of the blocks was counterbalanced across participants.

Results

The median correct response times were submitted to a mixed analysis of variance (ANOVA) with group (healthy adults and

Table 1
Age, Sex, Cause, Location of Lesions, and Neurological Signs of the Four Patients Who Served as Participants

Patient	Age/sex	Cause	Location	Neurological signs
PF	53/F	Stroke	Left parietal, extending to superior temporal cortex	Extinction
MH	48/M	Anoxia	Left inferior parietal, angular gyrus	Extinction, mislocalization
RH	70/M	Stroke	Left parietal (angular and supramarginal gyri), superior temporal gyrus	Anomia, extinction
MP	54/M	Aneurysm	Right parietal (angular gyrus, supramarginal gyrus)	Left neglect and extinction, hemiplegia

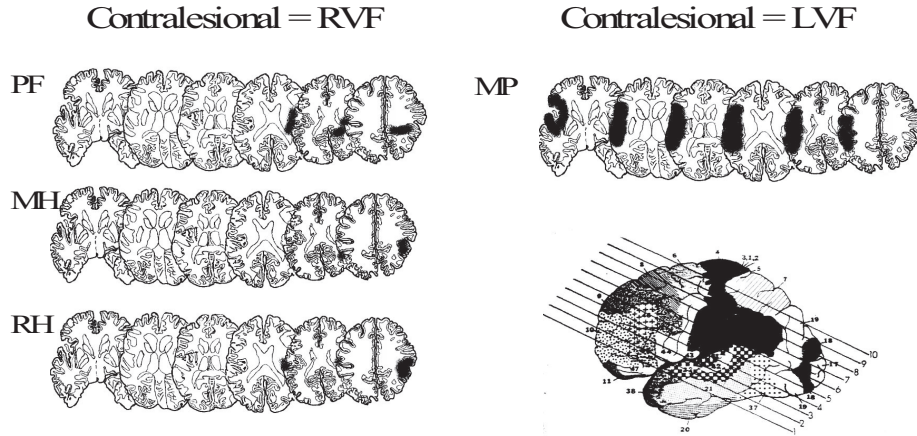


Figure 1. MRI scans plotted onto standardized slices of the four patients (MH, PF, RH, MP) who served as participants. The standardized plates are taken from Gado, Hanaway, and Frank (1979). Only slices 3 to 8 are depicted here.

patients) as the between-subjects factor and cue field¹ (ipsilesional and contralesional), target field (up and down) and cueing (cued and uncued) as within-subject factors (see Table 2). The results yielded significant main effects of group, $F(1, 7) = 8.41$, $MSE = 115793$, $\eta^2 = 0.954$, $p < .001$, and cueing, $F(1, 7) = 12.41$, $MSE = 134$, $\eta^2 = 0.639$, $p = .010$. Response times were higher for the group of patients (601 ms) compared with the healthy adults (367 ms), and for the cued object (488 ms) relative to the uncued object (479 ms). Also, the following interactions reached statistical significance: group by cue field, cue field by target field by cueing, and group by cue field by target field by cueing, $[F(1, 7) = 6.609$, $MSE = 148$, $\eta^2 = 0.486$, $p = .037]$, $[F(1, 7) = 17.1$,

$MSE = 114$, $\eta^2 = 0.710$, $p = 0.004]$, and $[F(1, 7) = 17.27$, $MSE = 114$, $\eta^2 = 0.712$, $p = 0.007]$, respectively. To analyze the four-way interaction, we conducted separate ANOVAs for each group with cue field (left and right for the healthy adults, and ipsilesional and contralesional for the group of patients), target field and cueing as within-subject factors.

The group of healthy adults showed a significant main effect of cueing, $F(1, 4) = 15.84$, $MSE = 40$, $\eta^2 = 0.798$, $p < .016$, response times were slower for targets presented in the cued object (371 ms) relative to the uncued object (363 ms). No other main effects or interactions yielded statistical significance, $ps > .05$. Although any interactions with target field were not reliable, separate ANOVAs for the “up” and “down” targets revealed that IOR was present for “up” targets only, $F(1, 4) = 23.82$, $MSE = 23.82$, $\eta^2 = 0.856$, $p = .008$, and $F < 1$, for “up” and “down” targets, respectively.

The group of patients showed a significant effect of cue field, and significant interaction of cue field by target field by cueing, $F(1, 3) = 17.62$, $MSE = 76$, $\eta^2 = 0.855$, $p = .025$, and $F(1, 3) = 28.81$, $MSE = 29$, $\eta^2 = 0.906$, $p = 0.016$, respectively. Response times were higher for targets appearing in a box that was originally cued in the ipsilesional field (607 ms), relative to the contralesional field (594 ms). Finally, the analysis of the interaction yielded a significant object-based IOR effect (a 46-ms effect) only for targets appearing in the “up” location box that was originally cued in the contralesional field, $F(1, 3) = 69.93$, $MSE = 62$, $\eta^2 = 0.959$, $p = .004$. This effect was present for each patient: IOR effects of 46, 36, 62, and 42 ms, respectively, for patients MH, PF, RH, and MP. There were no significant IOR effects for targets that appeared in the box that was originally cued in the ipsilesional field (effects of -8 and 19 ms for “up” and

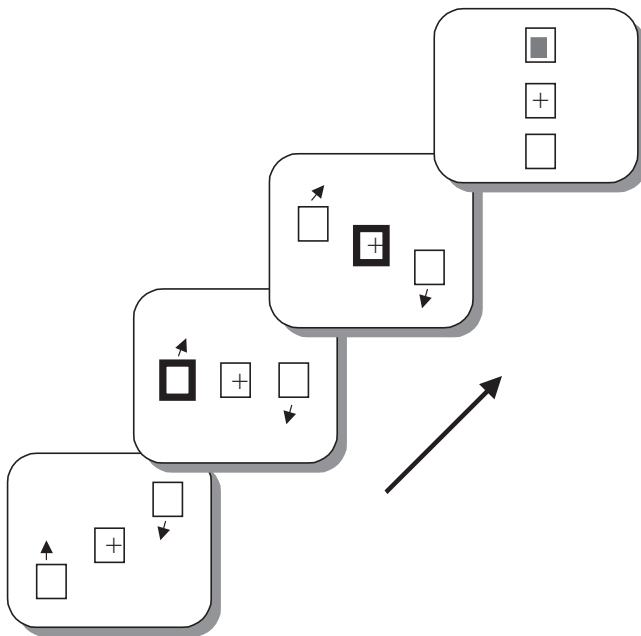


Figure 2. Sequence of events and exposure duration of stimuli for a cued with clockwise motion.

¹ The left hemifield was the ipsilesional hemifield for the patients MH, PF, and RH and the contralesional field for MP, and the right hemifield was the contralesional hemifield for the patients MH, PF and RH and the ipsilesional field for MP. Also, in order to match the controls with the patients, we randomly assigned the left visual hemifield to the contralesional condition for four of the controls and to the ipsilesional condition for one of the controls, and the opposite for the right visual field.

Table 2

Mean Response Times and Standard Deviation (SD) as a Function of Cue Field (Left and Right, Ipsilesional and Contralesional), Target Field (Up and Down), and Cueing (Cued and Uncued) for the Group of Controls and Patients

	Controls							
	Ipsilesional left		Cue		Contralesional		Cue	
	Target up		Target down		Target up		Target down	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Cueing								
Cued	382	89	357	70	375	80	369	54
Uncued	370	74	354	58	362	89	365	52
IOR	12		3		13		4	
	Patients							
	Ipsilesional		Cue		Contralesional		Cue	
	Target up		Target down		Target up		Target down	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Cueing								
Cued	585	133	635	195	625	172	581	177
Uncued	593	170	616	178	579	165	593	155
IOR	-8		19		46		-12	

Note. IOR, inhibition of return. IOR = Cued RT – Uncued RT (mean difference score).

“down” targets, respectively), and there were no IOR effects for targets that appeared in the “down” location and that were originally probed in the contralesional field (-12 ms of effect), $ps > .05$.

Given that the mean IOR effect for the “down” targets that were originally cued in the ipsilesional field (19 ms) was larger in magnitude than the mean IOR effects for “down” targets in the control group, we conducted further analyses to assess whether IOR decreased in magnitude or was eliminated in the ipsilesional field for the patients. We tested whether the 19-ms effect found for “down” targets cued in the ipsilesional field was reliably larger than the IOR effects observed in the control group. We conducted a mixed $2 \times 2 \times 2$ ANOVA with group as the between-subject factor, and cue field and cueing as within-subject factors just for the data from the “down” target conditions. The results showed only a main effect of group, $F(1, 7) = 9.05$, $MSE = 58948$, $\eta^2 = 0.953$, $p = .019$. Neither group showed an IOR effect for “down” targets.

Discussion

The results from the group of healthy adults replicated the object-based IOR effect found in previous studies (Tipper et al., 1991, 1994, 1997; McCrae & Abrams, 2001; Weaver et al., 1998), using a similar dynamic procedure to the one constructed by Tipper et al. (1994). The overall magnitude of the object-based IOR effect was small (8 ms), compared with the typically reported IOR effect with static stimuli. However, as noted by Tipper et al. (1991), the effects with static stimuli may reflect a combined influence of both object-based and location-based effects.

One new result with the controls (see Figure 3) is that, for the controls, IOR effects tended to be greater for stimuli that moved “up” than for stimuli that moved “down” (although not significant

in the overall ANOVA, separate tests revealed only significant IOR for “up” moving stimuli). We believe this is the first time that this result has been noted with control participants, although position of movement is not typically analyzed as a factor in control studies. However, the result may be a manifestation of the same process we observed with parietal patients, in which imbalances in attention modulate IOR effects. There is evidence that, in normal participants, attention in search tasks can be biased toward the upper visual field (Heywood & Churcher, 1980), perhaps because the upper field contains a representation of far space (Previc, 1990). If there is an attentional bias favoring items in higher

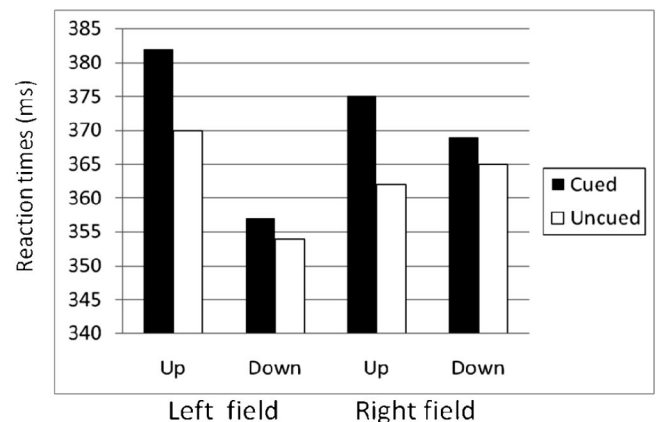


Figure 3. Mean reaction times (in ms) for cued and uncued trials as a function of cue field (left and right) and target field (up and down), for the control participants.

positions in the visual field, then it may be more difficult to subsequently inhibit stimuli that initially appeared at locations higher than their end position, leading to smaller IOR effects in the “down” condition here. The difference with the patients is that (a) the patients show an ipsilesional and contralesional distinction in IOR in addition to any distinction based on the height of items in the field, and (b) the ipsilesional and contralesional distinction is stronger than the “up” and “down” distinction observed in the controls.

The results from the group of patients (see Figure 4) showed an object-based IOR only when the cued box was presented in the contralesional field and moved in a contralesional to ipsilesional direction (a 46-ms effect for upper targets). There was no equivalent IOR effect when the cue box appeared in the ipsilesional field and moved in an ipsilesional to contralesional direction (overall, a 5-ms effect for the ipsilesional cue condition). When the cue was presented in the contralesional field, “down” targets failed also to exhibit significant IOR (an effect size of -12 ms). The implications of these findings for understanding the role of the parietal lobe in implementing inhibitory attentional biases are discussed below.

Location-Based IOR and the Parietal Lobe

Tipper et al. (1994, 1997) suggested that the neural systems underlying location-based and object-based IOR effects might be phylogenetically and neurally distinct. Location-based IOR may be associated with a phylogenetically old subcortical system responsible for oculomotor programs. In contrast, object-based IOR may be associated with a phylogenetically younger, cortical system capable of tracking object motion. The neural mechanisms underlying location-based IOR has been the focus of a heated debate during the last decades. Although previous studies tended to regard the collicular and cortical accounts as mutually exclusive, more recent studies support the idea of multiple mechanisms, collicular and cortical, contributing to IOR (Summer, 2006). With regard to involvement of the cortex in the generation of IOR, mounting evidence from neuroimaging (Lepsien & Pollmann, 2002; Rosen et al., 1999) and neuropsychological (Bartolomeo et al., 1999; Bartolomeo et al., 2001; Vivas et al., 2003; 2006) studies suggests that the parietal cortex (along with other brain regions) may play a

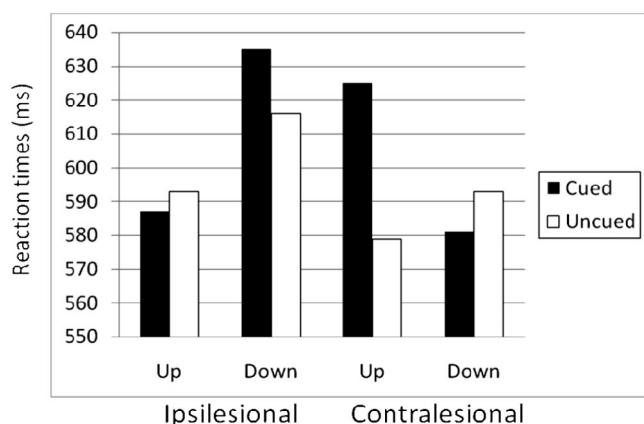


Figure 4. Mean reaction times (in ms) for cued and uncued trials as a function of cue field (ipsilesional and contralesional) and target field (up and down), for the patients.

crucial role. More specifically, Vivas et al. in 2003 and 2006 have proposed that attentional biases such as IOR would be implemented by the parietal lobe through spatial maps that represent locations as a function of the saliency of the items there. Spatially asymmetrical lesions to the parietal lobe are then held to produce an imbalance in the relative saliency of items, with the saliency of ipsilesional stimuli being increased relative to that of the contralesional stimuli. The net result of this is an unbalanced spatial competition for selection and, in particular, difficulty in inhibiting the locations of stimuli that appear (at least initially) on the ipsilesional side of space.

As we have mentioned in the Introduction, the idea of a master saliency map to guide attentional orienting is not new in the literature and has been successfully implemented in models of visual search (Heinke & Humphreys, 2003; Itti & Koch, 2000, 2001; Wolfe, 1994). Recently, a similar idea has been incorporated in a “real neuronal architecture” model developed by Shipp (2004) in order to explain IOR. Shipp (2004) has proposed that IOR would reflect reduced saliency of stimuli at recently explored locations. This mechanism would ensure that other locations in the visual field are able to compete for focal attention. However, Shipp (2004) proposed that reduced saliency to stimuli at cued locations would be mediated by a frontal and/or parietal loop through the superior colliculus to the ventral pulvinar which contains the saliency map. We propose that, perhaps in addition to ventral pulvinar (Shipp, 2004), relative saliencies are also represented within parietal cortex (Vivas et al., 2001; 2003). It is interesting to note that, unlike unilateral parietal lesions, unilateral lesions to the pulvinar nucleus do not abolish IOR (Sapir, Rafal, & Henik, 2002), suggesting that saliency representations may be even stronger at a parietal level. A lesion at the parietal level may be required to produce an imbalance in saliency that is sufficiently large to negate IOR to ipsilesional stimuli. On the basis of this idea, we propose that the deficit in location-based IOR found in our previous studies with patients who have parietal lesions can be explained in terms of increased saliency of ipsilesional signal, which would receive reduced competition from contralesional locations. The increased saliency of an ipsilesional signal in the spatial map would be high enough to overcome any inhibition applied to ipsilesional locations by these patients, after stimuli have been attended.

This hypothesis fits well with previous studies that have reported facilitation instead of inhibition for ipsilesional locations in neglect patients when a second central cue was not used to reorient attention back to the center (Bartolomeo et al., 1999; Bartolomeo et al., 2001). An alternative hypothesis may be that unilateral damage to the parietal lobe affects the generation of an inhibitory signal at the attended location in the contralesional field. However, this hypothesis would predict a pattern of impaired IOR opposite to the one observed in parietal patients; that is, IOR should be not observed in the contralesional field. Results from our previous studies of intact IOR in the contralesional field contradict this prediction.

Object-Based IOR and the Parietal Lobe

This same idea, of the increased saliency of ipsilesional stimuli overruling IOR, can also be applied to the case of moving stimuli. In the ipsilesional cue condition, an ipsilesional box is initially cued, which then moves toward midline. We hold that there is increased saliency for ipsilesional stimuli, which makes them

difficult to inhibit, even if objects can be tracked across the visual field. Any inhibition that is applied may be sufficient to take activation in the cued box down to a neutral baseline level (so performance is not facilitated), but insufficient to generate IOR. On this account, there is a common deficit affecting both location and object-based IOR, which may reflect disrupted location-IOR in the first place.

However, it is difficult to know exactly what to make of the lack of IOR for the contralesional cue when the target moved down the screen. For example, it cannot be the case that patients failed to orient attention to the contralesional stimulus in the first place, given that a cue in the contralesional box produced IOR when the box moved to the “up” location. One account of the result is based on the premise that, as well as directing attention to the location of static stimuli, the parietal lobe is also responsible for directing attention to other nonspatial properties of objects, such as their motion (Kusunoki, Gottlieb, & Goldberg, 2000; Colby & Goldberg, 1999; Culham et al., 1998). For instance, it has been reported that neurons, in the lateral inferior parietal lobe of monkeys, respond to moving objects, and that their activation is modulated by the task-behavioral relevance of the stimulus (Kusunoki et al., 2000). These neurons receive projections from motion-processing regions such as the middle temporal cortex (MT), and the middle superior temporal region (MST; Zeki et al., 1991), which are capable of coding speed and direction of motion. Previc (1990) has also argued that the parietal lobes direct attention into the lower field, so that a unilateral parietal lesion could lead to poor tracking of objects particularly when they move to the lower field. As a consequence, there is reduced IOR when the target appears in the lower visual field. However, it seems unlikely that poor tracking of moving objects could explain the differential IOR effects from contra- and ipsilesional cues that move to the “up” location. For example, we know of no evidence that the movement tracking is more difficult from the ipsilesional than from the contralesional space. In contrast, the idea that the salience of items originally presented in the ipsilesional space makes them difficult to subsequently inhibit can provide a parsimonious explanation of the deficit found in studies examining both environment-based and object-based IOR.

Finally, we note that previous studies have reported that older adults have difficulty in instantiating object-based IOR (McCrae & Abrams, 2001). The older participants in McCrae and Abrams’s study were generally older than the patients in our study (older participants’ mean age = 74 years; the mean of age of the patients in our study was 56.25 years), and only one of our patients was within the age range of the old participants in McCrae and Abrams. This patient, RH, showed a robust object-based IOR effect of 62ms when an object in his contralesional field moved into the “up” location. Note also that the patients were compared with age-matched controls. Hence, it is very unlikely that the our results reflect the ages of the patients.

Conclusions

Since IOR was first reported by Posner and Cohen (1984), much research has been conducted to investigate the nature and neural bases of this phenomenon. Our study provides a first analysis of object-based IOR in patients with parietal damage, and it provides evidence for a selective breakdown in object-based IOR. Although

IOR is spared for objects cued in the contralesional field that move into the upper visual field, there was no evidence for object-based IOR in other circumstances. We suggest that there may be at least two loci to the breakdown in IOR: (a) an increased salience for objects initially appearing in the ipsilesional field, which continues even when these stimuli move in space; and (b) a problem in attentive tracking of objects into the lower visual field.

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