

Object-Based Facilitation and Inhibition From Visual Orienting in the Human Split-Brain

Steven P. Tipper
University of Wales, Bangor

Robert Rafal
University of California, Davis

Patricia A. Reuter-Lorenz
University of Michigan

Yves Starrveldt, Tony Ro, Rob Egly,
and Shai Danzinger
University of California, Davis

Bruce Weaver
University of Wales, Bangor

Object-based attention was examined in 2 split-brain patients. A precued object could move within a visual field or cross the midline to the opposite field. Normal individuals show an inhibition in detecting signals in the cued object whether it moves within or between fields. Both patients showed this effect when the cued object moved within a visual field. When it crossed the midline into the opposite visual field, however, detection was faster in the cued box. These results reveal both facilitatory and inhibitory effects on attention that are object based and may last for several hundred milliseconds. However, the inhibition requires an intact corpus callosum for interhemispheric transfer, whereas the facilitation is transferred subcortically.

When attention is oriented to a location by a peripheral cue, such as the brightening of a box, two things happen. Initially, detection of targets in that location is facilitated (e.g., Posner & Cohen, 1984). As little as 300 ms later, however, detection of targets and eye movements toward the cued location are impaired relative to a previously uncued location (e.g., Abrams & Dobkin, 1994). This subsequent inhibition of return (IOR; Posner & Cohen, 1984) was the focus of our research.

IOR effects have now been observed in many different situations. They are obtained when observers report the onset of a visual or auditory target with a keypress response (e.g., Maylor, 1985; Reuter-Lorenz, Jha, & Rosenquist, 1996), when they make eye movements to the cued location (e.g., Abrams & Dobkin, 1994), when they respond to the color of the target object (Law, Pratt, & Abrams, 1995), when discriminating targets (e.g., Pratt, 1995), and when making temporal order judgments (Gibson & Egeth, 1994). Therefore, IOR is a pervasive effect that appears to influence a variety of sensorimotor tasks.

Steven P. Tipper and Bruce Weaver, Centre for Perception and Motor Sciences, School of Psychology, University of Wales, Bangor, Gwynedd, United Kingdom; Robert Rafal, Yves Starrveldt, Tony Ro, Rob Egly, and Shai Danzinger, Department of Neurology and Center for Neuroscience, University of California, Davis; Patricia A. Reuter-Lorenz, Department of Psychology, University of Michigan.

Correspondence concerning this article should be addressed to Steven P. Tipper, Centre for Perception and Motor Sciences, School of Psychology, University of Wales, Bangor, Gwynedd LL57 2DG, United Kingdom. Electronic mail may be sent via Internet to pss060@bangor.ac.uk.

The effect is not caused by low-level sensory masking of the target by the cue because it can be observed when the target is presented 3,000 ms or more after the cue (Tassinari, Aglioti, Chelazzi, Marzi, & Berlucchi, 1987; Tipper & Weaver, in press); and even when there is no target in the cued location and eye movements to that location are generated in response to central arrow cues (Abrams & Dobkin, 1994; Rafal, Egly, & Rhodes, 1994). Furthermore, the effect can be produced when no peripheral cue is presented, in situations in which an eye movement is made to the peripheral location, or even if the eye movement is just planned and then vetoed (Rafal, Calabrasi, Brennan, & Sciolto, 1989). Finally, the effect is not based on a low-level retinotopic frame of reference because it survives eye movements between cue and target presentation (Posner & Cohen, 1984).

The function of this IOR mechanism may be to facilitate the efficient movement of covert or overt attention to novel locations. The repeated sampling of the same location would appear to be an inefficient and potentially deleterious search behavior. This is particularly true when the attended location does not contain any information relevant to the organism's current behavioral goals. For example, when searching for food, a location devoid of food should be inhibited to prevent attention fruitlessly returning. Thus, IOR prevents the return of attention to recently examined locations, thereby ensuring that attention is oriented to novel ones. In this way, the environment can be searched efficiently for objects that are relevant to the organism's survival, such as food and predators.

Researchers have begun to further examine the frames of reference in which IOR functions. Tipper, Driver, and

Weaver (1991) and Tipper, Weaver, Jerreat, and Burak (1994) noted that the spatial- or environment-based frame of reference previously described is adequate when attention systems are searching for stationary objects. However, in many situations an animal may be searching for a moving object.

Consider, for example, a female chimpanzee searching for her young offspring in a group of moving animals or a human searching a crowd for the face of a friend. In such a situation, search mechanisms of excitation and inhibition that have access only to spatial frames of reference will be inadequate. Attention would be inhibited from returning to the location occupied by an object at the time attention was first drawn to it. Shortly afterward, however, the object will have moved to a new location and may be needlessly reattended.

Tipper et al. (1991, 1994) suggested that IOR can be associated with dynamic, object-based internal representations: As an object moves through space, the inhibition can move with it. Such a mechanism enables efficient search, even for mobile objects. In support of this idea, object-based IOR has been reported in several experiments (Abrams & Dobkin, 1994; Tipper et al., 1991, 1994).

Initially, Tipper et al. (1991) argued that IOR functioned in only one frame of reference, which is object based. Subsequent work, however, has shown that these initial conclusions were wrong. Tipper et al. (1994) have demonstrated that both location- and object-based IOR can exist simultaneously.¹ That is, attention is slower to orient both to a previously cued location, and to the object that was cued but has subsequently moved to a new location.

A number of contrasts between location- and object-based IOR have now been observed: First, the location-based effect can be associated with a featureless part of the computer screen. By contrast, the object-based effect is obtained only when the object is visible at the time of cuing; if it is occluded by another object when attention orients to the cue, no IOR is observed (Tipper et al., 1994). Second, Abrams and Dobkin (1994) have demonstrated that the location-based effect is associated with inhibition of the oculomotor system that controls saccades and with inhibition of perceptual systems that detect the onset of the target. By contrast, the object-based effect is associated only with inhibition of the perceptual detection system (see also Reuter-Lorenz et al., 1996). Third, Tipper and Weaver (in press) observed that location- and object-based IOR effects can be dissociated by manipulating the stimulus onset asynchrony (SOA) from initial cue to target. They examined location- and object-based IOR at SOAs of 598, 1,054, and 3,560 ms. The location-based effects at these SOAs were -18, -15, and -24 ms, respectively. As these numbers suggest, the location-based effect did not interact with SOA. However, a different pattern emerged for the object-based effects. Here, the three effects (in the same order) were -31, -15, and -1 ms, respectively. In this case, the interaction with SOA was highly reliable, $F(2, 72) = 13.58, p < .001, MSE = 231.51$. Thus, it would appear that location-based IOR is relatively long-lasting, whereas object-based IOR decays fairly quickly.

Finally, Tipper et al. (1994) speculated that the IOR observed in static displays and that associated with moving objects may be subserved by different neural systems: IOR in static displays is thought to be mediated by midbrain extrageniculate visual pathways, whereas object-based IOR in moving displays is controlled by the cortex. Evidence that the IOR in static displays is associated with the superior colliculus (SC) of the midbrain has been supported by converging observations in healthy individuals and patients with neurological damage. When healthy individuals view displays monocularly, there is a larger IOR effect when the cue appears in the temporal hemifield than when it appears in the nasal hemifield. This asymmetry reflects the structure of the afferent pathways to the midbrain (Rafal et al., 1989; Rafal, Henik, & Smith, 1991). Second, patients with progressive supranuclear palsy, which results in damage to the SC, are the only group of individuals with brain damage who do not produce IOR effects (Rafal, Posner, Friedman, Inhoff, & Bernstein, 1988). Other groups with lesions not involving the SC (e.g., Parkinson's, temporal lobectomy, parietal and frontal lesions) produce normal IOR (Posner, Rafal, Choate, & Vaughn, 1985). Finally, visual processing in the newborn is dominated by the SC, and IOR is obtained in infants just 1 day old (Valenza, Simion, & Umiltà, 1994; see also Clohessy, Posner, Rothbart, & Vecera, 1991).

By contrast, Tipper et al. (1994) suggested that the object-based IOR in moving displays is mediated by the cortex. For such effects to be observed, highly sophisticated motion analysis is required. A number of objects have to be tracked accurately as they move from one location to another. A review of the literature suggests that the SC may not be capable of the sophisticated motion analysis that could support such performance without support from cortical systems (Goldberg & Wurtz, 1972; Gross, 1991; Schiller, 1972). Certainly, while the SC remains intact, lesions to the visual cortex of a variety of species result in the loss of the motion perception that would be necessary for object-based IOR. By contrast, there is no evidence that lesions to the SC impair object motion perception as long as the middle temporal (MT) visual area is intact and receives other (cortical) inputs (Graham, Berman, & Murphy, 1982; Newsome, Wurtz, Dursteler, & Mikami, 1985; Palmer & Rosenquist, 1974; Wickelgren & Sterling, 1969).

As Schlag and Schlag-Rey (1983) noted, the SC units encode events (for the control of eye movements) in particular locations, whereas cortical systems are concerned with encoding object-based properties. Thus, it appears that cortical pathways through MT/V5 areas are necessary for the analysis of object speed and direction. Of most pertinence here, discrete cortical lesions in human participants can selectively disrupt the perception of object motion even

¹ In Tipper, Weaver, Jerreat, and Burak's (1994) article, they referred to "environment-based" frames of reference. We now prefer the term *location based* because it specifies what we mean more precisely. The environment with which an organism interacts contains many properties, such as objects and locations. It is these specific properties of the environment that can be associated with inhibition.

when subcortical structures are intact. For example, the patient studied by Zihl and colleagues (e.g., Shipp, de Jong, Zihl, Frackowiak, & Zeki, 1994; Zihl, von Cramon, & Mai, 1983) was unable to perceive the motion of objects even though many other perceptual processes were normal. By contrast, patients with lesions to the SC (e.g., patients with progressive supranuclear palsy) appear to be able to perceive object motion.

The purpose of our research was to determine whether subcortical structures could be the neural substrate for object-based IOR or whether cortical representations are required. We investigated object-based IOR in 2 split-brain patients who had undergone complete corpus commisurotomy for intractable epilepsy. The corpus callosum (CC) is a massive nerve tract containing 800 million fibers (Bogen, 1990). Its main function appears to be to provide direct connections between homologous regions of the cortical hemispheres. Sectioning of the CC prevents direct communication between the neocortices of the two cerebral hemispheres. Therefore, although CC section is not direct evidence for cortical involvement (only studies of discrete cortical lesions can demonstrate this), it is a strong marker for cortical involvement.

In one condition of the experiments to be reported here, after attention was cued to one of two peripheral objects, the objects rotated 90°. This rotation was such that the objects either remained within a visual hemifield or crossed the midline and entered the other hemifield. We hypothesized that if object-based IOR is mediated by cortical structures, and is communicated between hemispheres via the direct CC connections, then in the split-brain such inhibition will move with the object as long as it remains within one visual hemifield. In this situation, the inhibition associated with the object will be detected via responses to the target because both events take place within the same cortical hemisphere (see Figure 1A). However, if the object is cued and then crosses the midline into the opposite visual field, IOR may not be detected. That is, the inhibition associated with the object in one hemisphere will not be accessible to processing when the object subsequently appears in the opposite hemisphere because one hemisphere is unaware of the inhibition created in the other hemisphere (see Figure 1B). By contrast, if object-based IOR is subserved by subcortical structures such as the SC, it should be obtained regardless of whether object motion is within or between visual hemifields.

We also examined IOR after 180° of rotation. This is an interesting condition because previous data suggest that object-based and location-based effects compete. That is, when an object is cued, inhibition moves with the object through 180° to the opposite side of the screen. However, the uncued object moves into the location that was cued. Therefore, object-based IOR can be masked by the location-based IOR observed in the uncued object. Indeed, it is not uncommon to observe either smaller object-based IOR effects after 180° than after 90° rotations, and sometimes the effect vanishes completely (Tipper et al., 1994). We predicted very different results for split-brain patients, however. On 180° trials, both peripheral objects cross the midline between cuing and target presentation. Therefore, in these

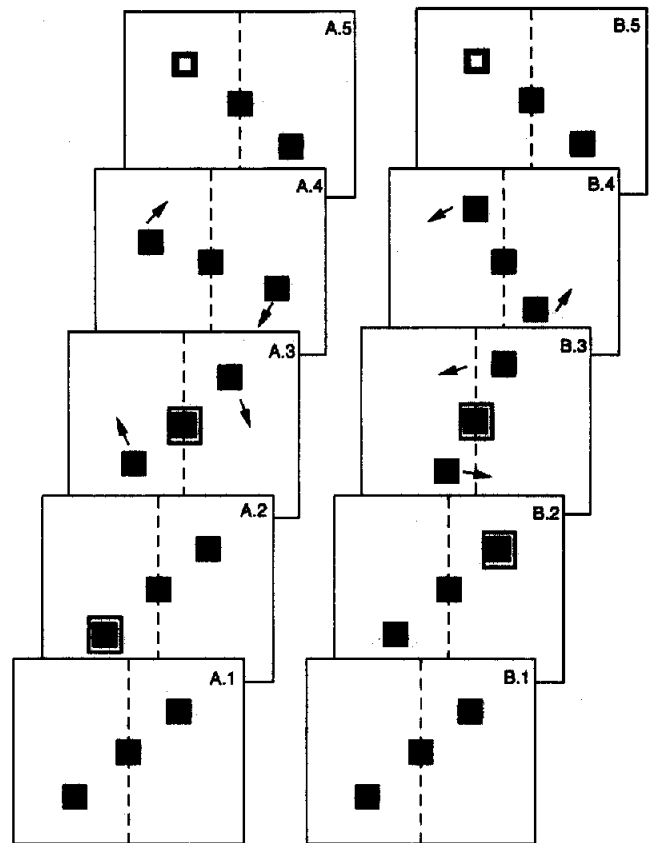


Figure 1. Depiction of the 90° rotation conditions. Figures 1A.1–1A.5 show the within-fields condition, where each peripheral object remained within the same hemifield throughout the 90° rotation. Figures 1B.1–1B.5 show the between-fields condition, where each peripheral object crosses from one hemifield to the other between the time of cuing and presentation of the target probe. The figure is not drawn to scale.

individuals, there should be no object-based IOR to oppose the location-based effect. We assumed that the latter would be intact. Therefore, reaction times (RTs) should be higher for targets in the uncued box after 180° of rotation because it will then occupy the cued location. Location-based IOR will be seen because there will be no object-based IOR to oppose it.

We conducted the first experiment to verify that the moving IOR effect was present in neurologically intact observers under the same conditions from which the data for the callosotomy patients were obtained. We found that in control observers, there was no difference in the magnitude of within-fields versus between-fields IOR.

Experiment 1

Method

Participants. Twenty undergraduates (mean age = 20.1 years) participated to earn credit for an introductory psychology course. They were naive about the purpose of the experiment. Each observer was tested individually in a single session that lasted about 30 min.

Apparatus. Stimulus presentation and the recording of RTs and error rates were controlled by a Packard Bell 386/33 microcomputer with a color video graphics array (VGA) monitor. Stimuli were presented in VGA medium-resolution graphics, which has a 640×350 pixel resolution and a 70 Hz refresh rate. Responses were made via microswitches interfaced to the computer via a digital input-output card. RTs were computed using Bovens and Brysbaert's (1990) TIMEX function.

Procedure. The procedure was generally the same as in Experiments 2 and 3 in Tipper et al. (1994). Each trial began with the presentation of a prompt to press the start key. After the start key was pressed, three black squares appeared on a light gray background, one in the middle and one on either side equidistant from the middle. (These filled squares subtended 0.9° horizontal and 1.0° vertical of visual angle at 45-cm viewing distance, and adjacent squares were 6.6° apart.) In the initial display, which remained on for 1,086 ms, the left square was positioned either 45° (in polar coordinates) above or below horizontal (see Figure 1, panels A.1 and B.1). If it was above horizontal, the right square was 45° below horizontal; if it was below horizontal, the right square was 45° above horizontal.

One of the peripheral squares was cued 1,086 ms after the start of the trial by "flickering" it. This flickering was accomplished by presenting a filled black square inside of a larger white square for 100 ms and then displaying the black square alone for 100 ms (see Figures 1A.2 and 1B.2). (The larger white square subtended 1.3° horizontal and 1.8° vertical of visual angle.) Two hundred milliseconds after the onset of the cue in the outer square, the central square was cued in the same manner for 86 ms (see Figures 1A.3 and 1B.3). At the same time, the peripheral squares began to move smoothly around the central square in either a clockwise or counterclockwise direction. The apparent motion of the outer squares was achieved as in the Tipper et al. (1994) experiments. Generally, each frame remained on for 43 ms. On two thirds of the trials, however, a probe was presented in one of the outer squares for 86 ms.

The probe was a small white square (0.4° horizontal \times 0.5° vertical of visual angle) superimposed on one of the outer squares for 86 ms. The SOA between the initial peripheral cue and the probe was equally likely to be 500 ms (for 90° rotations, see Figures 1A.5 and 1B.5) or 842 ms (for 180° rotations, not shown in Figure 1). Participants pressed the target key on a response box as quickly as possible if a probe appeared. When no probe appeared (one third of the trials), they made no response. Audible feedback was provided following incorrect responses. Responses that took longer than 1.5 s (from the onset of the probe) were considered incorrect. There were 48 practice trials and 336 test trials. The dependent measures were median RT (in milliseconds) and percentage of errors.

Design. The 90° and 180° trials were analyzed separately. The 90° trials conformed to a two-variable repeated measures design. The first variable, field, had two levels: within and between. For within trials, the two peripheral boxes remained in the same visual hemifield they occupied at the time of cuing. This would be the case if the left box started 45° above horizontal and the rotation was counterclockwise or if the left box started 45° below horizontal and the rotation was clockwise. For between trials, the peripheral boxes crossed from one hemifield to the other. This would be the case if the left box started 45° below horizontal and the rotation was counterclockwise or if the left box started 45° above horizontal and the rotation was clockwise. The final variable, cuing, also had two levels: uncued and cued.

For the 180° trials, the within versus between distinction did not apply because both peripheral boxes always had to cross the

midline. Therefore, the 180° trials were examined only for uncued versus cued differences.

Results and Discussion

Errors occurred on less than 1% of the trials and were not analyzed further. Mean median RTs (for correct responses) for the 90° conditions are shown in Figure 2A. A two-variable repeated measures analysis of variance (ANOVA) revealed no significant effect of field, $F(1, 19) = 1.53$, $MSE = 152.70$, *ns*. However, the overall IOR effect (uncued minus cued) was significant, $F(1, 19) = 6.76$, $p < .001$, $MSE = 225.15$. The Field \times Cuing interaction was not significant ($F < 1$). In the within condition, object-based IOR was shown by 70% of the observers (mean size = -8 ms) and was significant by a planned contrast, $t(19) = 4.198$, $p < .001$. In the between condition, IOR was shown by 65% of the observers (mean size = -9 ms) and was again significant, $t(19) = 4.722$, $p < .001$.

The mean median RTs (correct responses only) for the 180° rotation uncued and cued conditions were 302 and 303 ms, respectively. This difference was not significant ($t < 1$). As before, the error rates were too low to analyze.

The data from these 20 healthy undergraduates support our initial assumptions. Although the IOR effects were small, they replicated our previous findings: Object-based IOR was observed after 90° of rotation, but not after 180° of rotation, presumably because object-based and location-based effects oppose each other. Of more relevance, whether

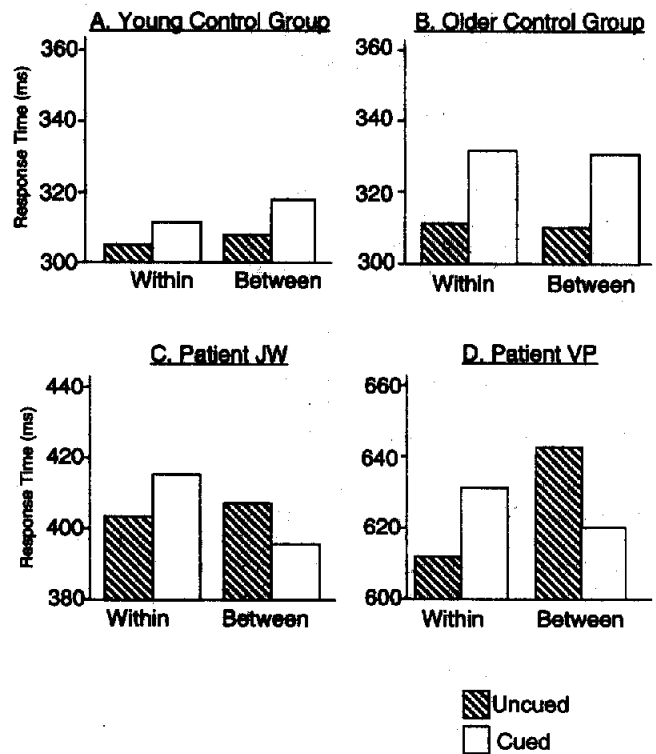


Figure 2. Reaction time (RT) data for the 90° trials. A: Mean median RTs for the neurologically intact undergraduates run in Experiment 1. B: Mean median RTs for the older control group run in Experiment 2. C and D: Mean RTs for J.W. and V.P., respectively.

an object remained within a hemifield or crossed the midline had no impact on object-based IOR.

Experiment 2

In this experiment we examined object-based IOR in 2 split-brain patients. Recall that if object-based IOR is mediated by cortical structures that communicate via the CC, we predicted that IOR would be observed only when the moving objects stay within the same hemifield. When the inhibited object crosses the midline, IOR will no longer be observed. Furthermore, in contrast to the null results observed in the 180° motion condition of Experiment 1, we predicted that there would be location-based IOR in the split-brain patients. Finally, as a further contrast with the split-brain patients, we tested another group of control participants. However, these individuals were substantially older and enabled an examination of the generality of the IOR effects in intact individuals.

Method

Participants. The 2 split-brain patients tested in this experiment both had undergone total callosotomy for treatment of intractable epilepsy. The surgery completely transected the entire CC but spared the anterior commissure, as confirmed by magnetic resonance (MR) imaging. J.W. was a 40-year-old man, and V.P. was a 42-year-old woman. Clinical, neuropsychological, and radiological findings in these 2 patients were as follows: J.W. underwent two-stage callosotomy at age 26. Preoperatively, his interictal neurological examination was normal, as were contrast-enhanced computed tomography (CT) results and cerebral spinal fluid analysis. Electroencephalographic (EEG) results indicated bilateral polyspike-and-wave paroxysms with a right anterior temporal predominance and occasional independent left frontoparietal spikes. Extensive postoperative testing indicated left hemisphere dominance for speech and the absence of visual and tactile transfer. Complete callosal section was confirmed by midsagittal MR imaging (Gazzaniga, Holtzman, Deck, & Lee, 1985). Testing carried out in 1988 indicated that J.W.'s Verbal IQ was 97, Performance IQ was 95, and Wechsler Memory Quotient (WMQ) was 102.

V.P. underwent a two-stage callosotomy at age 23 for a mixed seizure disorder. Preoperative EEG results showed left temporal sharp waves superimposed on diffuse spike and wave activity. CT results were normal. Postsurgical neuropsychological testing indicated left hemisphere speech lateralization with an absence of visual and tactile-motor interhemispheric transfer. One year after the surgery, limited right hemisphere speech was documented. Midsagittal MR imaging documented callosal remnants in the rostrum and splenium (Gazzaniga et al., 1985). Testing carried out in 1989 indicated a Verbal IQ of 81 and a WMQ of 93.

J.W. was tested in 16 experimental blocks (8 with each hand) over a 3-month period. V.P. was tested in 10 experimental blocks (5 with each hand) in two sessions several weeks apart.² Nine older control individuals (5 men and 4 women) ranging in age from 54 to 76 years ($M = 64$, $SD = 7$) also participated in this experiment.

Apparatus. Stimulus presentation and the recording of RTs and error rates were controlled by an IBM-compatible 486 microcomputer connected to a NEC Multisync color VGA monitor. The resolution of the monitor and the timing of the visual displays were the same as in Experiment 1. Responses were made on a two-button response pad interfaced to the computer by means of a standard

gameport. One button on the response pad was used by the participant to initiate a block of 12 trials, and another was used by the participant to make responses to target signals. Millisecond timing, used to obtain response latencies, was again achieved using Bovens and Brysbaert's (1990) TIMEX function.

Procedure and design. The procedure and design were the same as in Experiment 1. Note, however, that the 180° condition was not included for the 9 control participants in this experiment. They were originally tested as controls for patients with unilateral strokes. Because the purpose of that experiment was to compare the movement of IOR in the ipsilesional and contralesional visual fields, it required twice as many 90° trials in each session. The 180° condition was dropped because it would have been uninformative in that context and would have placed an additional burden on the stroke patients.

Results

Control group. Errors occurred on fewer than 2% of the trials and were not analyzed further. The means of median RTs for correct responses are shown in Figure 2B. A two-variable repeated measures ANOVA revealed no significant effect of field, $F(1, 8) = 0.481$, $MSE = 34.0312$, *ns*. The effect of cue was significant, $F(1, 8) = 12.065$, $p < .01$, $MSE = 8,288.2812$, in that detection was slower for targets appearing in the cued than in the uncued objects. The Field \times Cueing interaction was not significant, $F(1, 8) = 0.031$, $MSE = 3.3368$, *ns*. The size of the IOR effect was -22 ms for within-fields rotations and -21 ms for between-fields rotations.³

Patient data. Separate analyses were done for the 90° and 180° rotation conditions. The mean RTs for correct responses in the 90° rotation condition are shown in Figures

² The split-brain patients participated in both left- and right-hand trial blocks. Because the field of target presentation varied randomly within each trial block, responses were generated using a response hand that was either ipsilateral or contralateral to the hemisphere that received the target. For example, when the target was presented to the left hemisphere, the contralateral response hand was used in the right-hand response blocks, whereas the ipsilateral response hand was used during left-hand trial blocks. There appears to be some variation among split-brain patients in the pathways by which the separated hemispheres generate responses with the ipsilateral hand, with some individuals transferring what appears to be a sensory signal to the opposite hemisphere subcortically and others using an ipsilateral motor pathway (Clarke & Zaidel, 1989). Results of studies with the patients who participated in the current investigation indicate that an ipsilateral motor pathway rather than sensory transfer mediated these responses (Reuter-Lorenz, Nozawa, Gazzaniga, & Hughes, 1995; Seymour, Reuter-Lorenz, & Gazzaniga, 1994; see also Hughes, Reuter-Lorenz, Fendrich, & Gazzaniga, 1992).

³ As can be seen in Figure 2, the object-based inhibition of return (IOR) effect was somewhat larger in the older than the younger observers in Experiment 1. We have observed this pattern previously. For example, when correlating object-based IOR with age, we have found significant effects, in which the IOR was larger in older participants. Surprisingly, these correlations were obtained in a narrow age range (18–35 years) in a sample of 200 participants. Note also that McDowd, Filion, Tipper, and Weaver (1995) observed larger IOR in elderly individuals than in a group of college students.

2C and 2D for J.W. and V.P., respectively. Each patient's data were analyzed separately using 2×2 (Field \times Cue) repeated measures ANOVAs.

J.W. erred on fewer than 3% of the trials. Analysis of J.W.'s RT data from the 90° rotation condition (excluding incorrect responses) revealed a significant effect of field, $F(1, 15) = 11.17, p = .005, MSE = 1,564.5020$. RTs were lower when the boxes crossed the midline (403 ms) than when they moved within a hemifield (410 ms). The main effect of cue was not reliable, $F(1, 15) = 0.209, MSE = 50.627, ns$. However, there was a significant Field \times Cue interaction, $F(1, 15) = 10.11, p < .01, MSE = 4,435.6426$. As can be seen in Figure 2C, J.W. did show normal IOR when the boxes rotated within a hemifield, $t(15) = 2.293, p < .05, MSE = 1,769.2539$, but not when they crossed the midline. Rather, for between-fields movements, RTs were actually significantly lower in the cued box than in the uncued box, $t(15) = 2.808, p < .025, MSE = 2,717.0156$.

Analysis of J.W.'s RTs for correct responses in the 180° rotation condition revealed a significant effect of cue, $F(1, 15) = 5.471, p < .05, MSE = 3,507.0312$, in that RTs were shorter for targets appearing in the cued box (408 ms) than for targets appearing in the uncued box (418 ms).

V.P.'s error rate was less than 4%. Analysis of V.P.'s RTs for the 90° rotation conditions (excluding incorrect responses) revealed no main effect of field, $F(1, 9) = 1.39, MSE = 670.11, ns$. The main effect of cue also was not reliable, $F(1, 9) = 0.02528, MSE = 167.1139, ns$. However, like J.W., V.P. showed a significant Field \times Cue interaction, $F(1, 9) = 14.90, p < .005, MSE = 320.34$. She showed object-based IOR when the boxes moved within a hemifield, $t(9) = 2.850, p < .025, MSE = 276.87$, but facilitated responding to cued targets when the boxes crossed the midline, $t(9) = 3.467, p < .01, MSE = 210.59$.

In V.P.'s 180° RT data, there was a trend, similar to that observed for J.W., for RT to be lower for targets appearing in the cued box (650 ms) than for those appearing in the uncued box (662 ms). However, this difference was not statistically reliable, $F(1, 9) = 1.08, ns$.⁴

Discussion

In these two experiments, healthy young and old control observers showed object-based IOR both when objects moved within a visual hemifield and when they crossed from one visual field to the other. The 2 split-brain individuals also showed object-based IOR when the cued object moved within a visual field. However, they failed to show IOR when the object moved from one visual field to the other. Such results support our hypothesis that an intact CC providing direct communication between the cortical hemispheres is necessary for such effects to be transferred from one side of space to the other. As discussed, this provides a clear marker for cortical involvement in object-based IOR in moving displays.

Clearly, however, another aspect of our data was not predicted: Not only did the split-brain participants fail to show object-based IOR when the objects crossed from one visual field to the other, but they actually showed facilitation

for the cued object in this case. That is, removal of the inhibition associated with the object as it moved from one cortical hemisphere to the other revealed an underlying excitation that facilitated performance.

In the 180° rotation conditions, both patients showed shorter RTs for the cued object than for the uncued object (although this effect was not statistically reliable in V.P.). Previous studies (e.g., Tipper et al., 1994) with neurologically intact participants have shown that the 180° condition can exhibit a variety of effects: a small object-based IOR, no significant effect, or a small location-based IOR. Tipper et al. have attributed this mixed bag of results to the coexistence of two effects. The observed result in a particular experiment will depend on the relative strengths of the object-based and location-based IOR effects. If one of the two is dominant, an IOR effect may be observed, but if the two are equal in strength, there will be no significant effect.

The RT advantage shown by split-brain patients for targets appearing in the cued object after 180° rotations may reflect (a) the facilitatory effect for cued objects crossing the midline (as in the 90° condition); (b) location-based IOR at the cued location, as originally predicted by Tipper et al. (1994); or (c) both of these acting conjointly. There was no basis for distinguishing the relative contributions of these mechanisms in this study.

In summary, Experiment 2 had two major results. First, object-based IOR crossed from one hemifield to the other in normal individuals but not in split-brain patients. Thus, some cortical contribution is implicated for the representation sustaining object-based IOR, and the CC is required for transferring this representation between hemispheres. Second, when object-based IOR was eliminated in the between-fields movement of objects, an underlying facilitatory effect was revealed.

A possible interpretation of the within-fields IOR and between-fields facilitation lies in whole hemifield inhibition. For both patients, if we simply considered whether a target was presented in the hemifield that was cued, we would see

⁴ Whereas healthy observers showed object-based inhibition of return (IOR) for both within- and between-fields object movements (i.e., for 90° rotations), both split-brain patients showed object-based IOR only for within-fields movements. For between-fields movements, IOR was not present; instead, a facilitatory effect was evident for target probes appearing in cued objects that had crossed the midline. However, the 2 split-brain patients did differ from each other in one respect: J.W. showed a main effect of field, with reaction times (RTs) being shorter when the boxes crossed the midline (irrespective of cue), whereas V.P. did not show this difference. To determine whether this difference between the 2 patients was reliable and independent of the effects of cuing, we tested both patients in an experiment that was identical to the main experiment except that no cues were presented. J.W. was tested in eight blocks and V.P., in six blocks. Neither patient made more than 4% errors in this experiment. J.W., as in the main experiment, had faster RTs on trials in which the boxes moved between fields (376 ms) than when the boxes moved within the same hemifield (389 ms), $F(1, 7) = 49.1, p < .001, MSE = 16,584.61$. V.P., as in the main experiment, did not show this pattern: RTs for within- and between-fields movements did not differ ($F < 1$).

the following pattern: Targets occurring in the cued hemifield would be responded to more slowly than targets appearing in the uncued hemifield. Our comparison of cued and uncued objects was confounded with whether that object occurred in the cued or uncued hemifield. That is, in the within-fields movement condition where we found IOR, cued objects in a cued hemifield were associated with slower RTs than uncued objects in an uncued hemifield. Likewise, in the between-fields movement condition where we found facilitation, uncued objects in the cued hemifield were associated with slower RTs than cued objects in the uncued hemifield. In both cases, the slower RTs were associated with objects occurring in the cued hemifield. Is it possible, then, that the effects we observed were attributable to what might be described as whole hemifield IOR rather than object-based inhibition and facilitation?

There are at least two reasons why we think this is not the case. First, these same 2 patients demonstrated pronounced costs plus benefits within each hemifield for both predictive and nonpredictive peripheral cues at short SOAs (Reuter-Lorenz & Fendrich, 1990). This result indicates that lateralized cues do not simply affect the whole hemifield in split-brain patients (see also, e.g., Holtzman, Sidtis, Volpe, Wilson, & Gazzaniga, 1981). Second, in many studies that we have carried out using this paradigm in normal observers, we have never had any indication of whole hemifield effects. Although this does not preclude the possibility that such an effect could emerge in the callosotomized brain, previous studies of attention in these patients suggest that whole hemifield effects are unlikely.

Nevertheless, we thought it worthwhile to conduct another study to rule out the possibility that IOR in the split-brain is associated with an entire hemifield. In the next experiment, four boxes were presented in the four corners of an imaginary square, and IOR was examined after one of the boxes was cued. If IOR in the split-brain is associated with a specific location or object, RTs should be longer at the cued box relative to the three uncued boxes, and, importantly, the three uncued boxes should not differ. By contrast, if IOR is associated with the entire cued hemifield in the split-brain, then RTs to detect targets in the uncued box in the cued hemifield should be longer than for the two uncued boxes in the uncued hemifield.

Experiment 3

Method

Apparatus. Stimulus presentation and data collection were controlled by a Macintosh IIfx computer equipped with an Apple 15-in. (38.1 cm) color monitor that yielded a 640 × 480 pixel resolution. Responses were made via a peripheral response button mounted on a Plexiglas box that was connected to a Macpacq data acquisition system. Response sampling occurred at a rate of 1000 Hz and was synchronized with target onset.

Procedure. Each trial began with the onset of the fixation box (1° × 1°) and four boxes (1° × 1°) positioned at the corners of an imaginary square centered on the fixation point. At a viewing distance of 57 cm, the center of each box was 4.7° above or below and 4.7° to the left or right of the fixation box. Five hundred milliseconds after the appearance of the fixation box and the four

peripheral boxes, one of the peripheral boxes flickered for 100 ms. This flickering served as the cue. One hundred milliseconds after cue offset, the fixation box flickered for 86 ms. After a delay of 214 ms the target, a small white box, appeared for 86 ms at the center of one of the peripheral boxes. The cue-target SOA was 500 ms. The intertrial interval was 1,500 ms timed from the observer's response. On catch trials (20 of 140 trials), in which no target was presented, the start of a new trial occurred 1,500 ms after cue onset. V.P. participated in eight blocks of 140 trials, four blocks with each hand. Response hand was counterbalanced between blocks. Twenty-minute breaks were given after every two blocks. Testing was carried out in a single testing session.

Results and Discussion

For each condition a median RT for correct responses was calculated for each block. The medians were based on RTs in the range of 150 to 1,622 ms. V.P. had only three false alarms (a keypress on a catch trial) out of a possible 120 catch trials over the eight blocks. She failed to respond on 8.3% (80 of 960 trials) of the target-present trials. Analysis of the RTs using a repeated measures ANOVA had responding hand (left or right) as a between-groups variable. Cue condition (valid cue, invalid within field, and invalid between field) and field of target (left or right) were within-groups variables.

There was a main effect of cue condition, $F(2, 12) = 16.541$, $p < .001$, with slower target detection at the cued location (same-location condition = 494 ms) than at either the noncued location in the same visual field (within-fields condition = 453 ms) or the noncued location in the opposite visual field (between-fields condition = 460 ms). Planned comparisons revealed that the difference between the same-location (cued) and within-fields (uncued) conditions was significant, $t(3) = 6.696$, $p < .01$, and the difference between the same-location (cued) and between-fields (uncued) conditions was marginally significant, $t(3) = 3.071$, $p = .053$. The difference between the within- and between-fields uncued conditions was not significant ($p = .345$). Thus, the IOR was clearly evident in both the within-fields and between-fields conditions, indicating that IOR does not affect an entire hemifield.

There was an interaction between the responding hand and cue condition, $F(2, 12) = 4.861$, $p < .05$. For right-hand responses, target detection was slower in the same-location condition (474 ms) than in either the within-fields (436 ms) or between-fields (422 ms) conditions, but IOR tended to be greater in the between-fields condition than in the within-fields condition. For left-hand responses, the opposite was true: Target detection also was slower in the same-location condition (513 ms) than in either the within-fields (469 ms) or between-fields (498 ms) conditions; however, in this case, the within-fields IOR was greater than the between-fields IOR.

Finally, responding hand interacted with target field, $F(1, 6) = 6.316$, $p < .05$, such that left-hand responses were faster for left visual field targets (470 ms) than for right visual field targets (517 ms) and right-hand responses were faster for right visual field targets (440 ms) than for left visual field targets (447 ms). Neither difference was statisti-

cally significant. This pattern represents the advantage that is typically evident in these patients when the response can be initiated directly by the hemisphere contralateral to the response hand (e.g., Reuter-Lorenz, Nozawa, Gazzaniga, & Hughes, 1995).

General Discussion

The results of Experiment 3 are clear. They unequivocally show that IOR was associated only with the specific box cued. The inhibition was not associated with the entire hemifield cued. Therefore, our alternative and preferred explanation of the facilitation observed in split-brain patients when cued objects crossed the midline is that the uninformative cues used in this experiment must have activated two independent effects: an object-based IOR, which requires callosal transfer, and an object-based excitation, which can persist, like the IOR, for several hundred milliseconds but that can be transferred subcortically. In the healthy observers, the IOR effect typically dominated at the cue-target intervals used in these experiments; however, the excitation component was nevertheless present and might have been manifested as facilitated target detection under circumstances that removed the effects of the IOR.

This account is contrary to one possible interpretation of the effects of peripheral cues. The following pattern of events has been envisaged: Initially, attention is oriented to the periphery by the exogenous cue. Processing of stimuli is then facilitated (but see Tassinari, Aglioti, Chelazzi, Peru, & Berlucchi, 1994). Subsequently, a central cue is presented and attention is reoriented to the center of the display. One possibility is that excitation at the initially cued location rapidly declines when attention is drawn away and inhibition simultaneously begins to develop, which prevents the return of attention to that location (see Figure 3A). Clearly, then, when the target was presented at the 500-ms SOA used in Experiments 1 and 2, performance for cued targets was impaired. In split-brain patients, inhibition no longer acted on the moving object as it crossed the midline, so there should have been no difference between uncued and cued trials (see Figure 3B).

In sharp contrast, the facilitation observed when the cued object crossed the midline suggests a different series of processes. Thus, after attention was oriented to an object by a peripheral cue, the following events happened: Initially, the internal representations of the object were excited, producing the faster detection of targets associated with the object at short SOAs. However, this excitation did not rapidly decay upon onset of the central cue. Rather, even though attention was oriented to the central location, the excitation associated with the cued object remained and declined much more slowly. Thus, inhibition did not replace excitation but was simultaneously associated with the object (see Figure 3C).

In cuing paradigms of this sort, the facilitatory and inhibitory effects are conventionally inferred from a difference in performance for probes occurring at cued and uncued locations. If performance is better for probes at the cued location (or object), the conventional interpretation is

that excitation is present. If performance is worse for probes at the cued location (or object), inhibition is inferred. The model being applied here allows that excitation and inhibition may be independent mechanisms that influence performance at the same locus simultaneously. Thus, observed behavior is the net effect of two processes, one excitatory and one inhibitory. Note that this is by no means a new idea, especially in the area of classical conditioning (e.g., Pavlov, 1927; Solomon & Corbit, 1974; Spence, 1936, 1937) and other models of attention (e.g., Houghton & Tipper, 1994; Posner & Cohen, 1984; Rafal & Henik, 1994).

However, the current experiments have enabled us to observe that excitation does in fact continue to be associated with the cued object. When the cued object crosses the midline, the excitation associated with it is transferred from one hemisphere to the other subcortically. However, the inhibition is not transferred (see Figure 3D) because there is no callosal connection between the two hemispheres. As a result, the observed behavior is driven by the excitatory process alone. Our results converge with other recent findings that indicate that excitation and inhibition from uninformative cues are independent phenomena that can be manifest concurrently (e.g., Gibson & Egeth, 1994; Tassinari et al., 1994).

Note also that this two-process model of IOR dictates that small, and even null, effects must be interpreted with great caution (see, e.g., Müller & von Mühlhausen, 1996, who questioned the functional significance of object-based IOR on the grounds that it is a small effect). A small effect does not necessarily indicate that the underlying inhibitory process is weak. It may simply indicate that the underlying excitatory and inhibitory processes are roughly equal in strength.

In the dynamic displays used in this research, the objects could be distinguished only on the basis of their differing locations and unique motion trajectories. The objects could not be distinguished from one another on the basis of shape information because both objects were identical squares. Therefore, our results do not imply that form information *per se* is transferring subcortically. Indeed, there is a good deal of evidence from split-brain studies to indicate that form information cannot be communicated between the separated hemispheres (Corballis, 1995; Holtzman, 1984; Seymour, Reuter-Lorenz, & Gazzaniga, 1994). There is, however, at least one report supporting the idea that the perception of apparent motion can transfer across the vertical midline (Ramachandran, Cronin-Golomb, & Myers, 1986; however, see Gazzaniga, 1987). One of our patients (J.W.) was tested for the perception of apparent motion. This was normal within visual fields, but there was no perception of motion between fields. Nevertheless, even though apparent motion was not experienced between visual fields by one of the patients, our data indicate that information processed from our dynamic display was sufficient to support the transfer of object-based facilitation across the visual midline. The medium of this information transfer remains to be identified.

Our finding that object-based facilitation transfers but object-based IOR does not indicates that these effects must rely on different neural substrates. At this time we can only

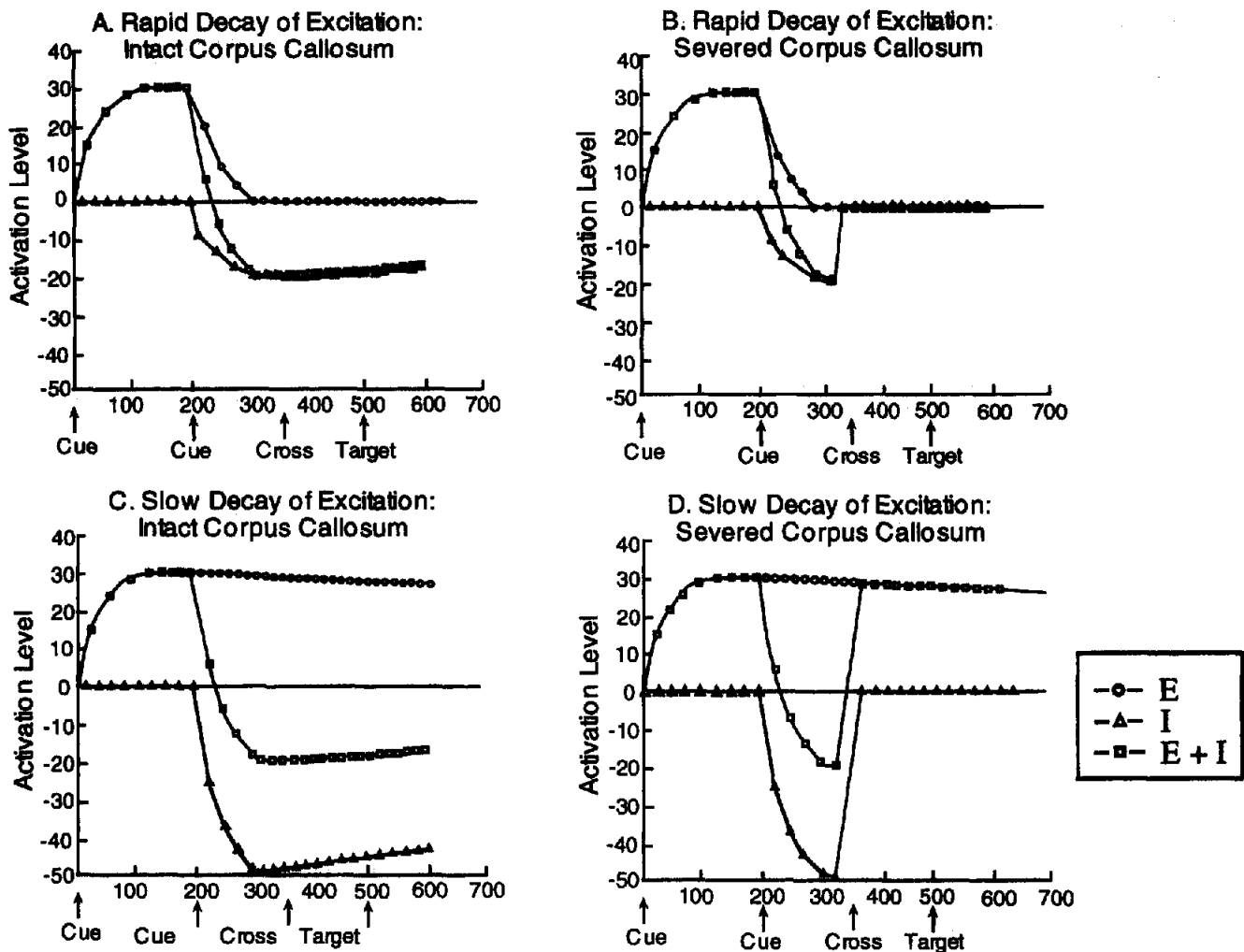


Figure 3. Schematic diagram of the processes underlying inhibition of return. A: Excitation decays rapidly after attention is oriented away from the peripheral location upon onset of the central cue. When the target is presented, only inhibition remains. B: The same situation for a split-brain patient. Again, excitation decays quickly after attention is drawn away from the peripheral location. However, now inhibition also vanishes when the cued object crosses the midline because there is no means of transferring the inhibition from one hemisphere to the other. C: Excitation does not decay rapidly when attention is oriented to the central cue. Rather, excitation lasts for at least 500 ms and coexists with inhibition. The observed behavior is the net effect of these two processes. Inhibition of return is normally observed because we assume that the later developing inhibition is more powerful at the time of target presentation. D: The pattern of excitation and inhibition suggested by the data obtained in Experiment 2 when the object crosses the midline. For split-brain observers, inhibition ceases to be associated with the object as its representation moves from one cortical hemisphere to the other, whereas excitation continues to move with the object's representation. E = excitation; I = inhibition.

speculate about what these neural substrates might be. It is likely that IOR relies to a greater extent on collicular processing than do the facilitatory precuing effects. The inability to transfer dynamic, object-based IOR may indeed reflect the relatively primitive motion analysis capabilities of the SC, as we outlined in the introduction. On the other hand, the transfer of information underlying the facilitation effect may be mediated via subcortical routes that do not involve the SC. One candidate pathway is the cortico-

pontine-cerebellar route (Glickstein, 1990). In primates, the cerebellum receives input from regions of the temporal and parietal cortex by way of the pons. Moreover, in the cat, some of these cortical-recipient units in the pons are directionally selective but lack orientation tuning. Although the output from the pons is primarily to the contralateral cerebellum, there is a sizable ipsilateral projection that, according to Glickstein (1990), could provide a basis for sensorimotor integration in the bisected brain.

An alternative route could involve the anterior commissure, which interconnects regions of the temporal lobe and remained intact in J.W. and V.P. Little is known about the function of this pathway. Interestingly, because the patients in the original West Coast commissurotomy series were lacking this structure, we would expect that those patients would not show transfer of the object-based facilitation if the anterior commissural pathway mediated this effect.

Conclusion

Our initial concern in this research was to confirm the role of the CC in the transfer of object-based IOR between visual fields, which provides support for our hypothesis that object-based IOR is mediated by cortical systems. The unexpected observation of facilitation when cued objects crossed the midline cannot be explained by whole hemifield inhibition in the split-brain. Rather, our preferred explanation relates to coexisting excitation and inhibition associated with object-based representations that are mediated by different neural structures. We must emphasize, however, that these theoretical proposals are tentative and that we are currently seeking converging evidence to test them.

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