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Unilateral Right Parietal Damage Leads to Bilateral Deficit for High-Level Motion

Case Study

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Summary

Patients with right parietal damage demonstrate a variety of attentional deficits in their left visual field contralateral to their lesion. We now report that patients with right lesions also show a severe loss in the perception of apparent motion in their "good" right visual field ipsilateral to their lesion. Three tests of attention were conducted, and losses were found only in the contralesional fields for a selective attention and a multiple object tracking task. Losses in apparent motion, however, were bilateral in all cases. The deficit in apparent motion in the parietal patients supports previous claims that this relatively effortless percept is mediated by attention. However, the bilateral deficit suggests that the disruption is due to a bilateral loss in the temporal resolution of attention to transient events that drive the apparent motion percept.

Introduction

Many studies have indicated the importance of parietal cortex in attention (cf. Corbetta et al., 1998). In particular, following damage to the right parietal region, patients often exhibit hemilateral neglect, including serious deficits in attentional processing in the contralesional visual field (Posner et al., 1984). In this paper, we contrast the performance of parietal patients to normal subjects on two high-level motion tasks in order to determine the extent and nature of attentional processing underlying these tasks.

Much of our perception of motion appears to be effortless, as if little in the way of attention is required. However, there are two well established motion systems (Julesz, 1971; Braddick, 1974; Anstis, 1980; Cavanagh, 1992; Lu and Sperling, 1996): a low-level system (or systems, according to Lu and Sperling, 1996) that is indeed effortless, passive, and preattentive, and a high-level system that appears to require attention (Cavanagh, 1992; Lu and Sperling 1996). Evidence of two separate motion systems was first presented by Wertheimer (1912), and modern research (e.g., Verstraten et al., 2000) continues to confirm this notion. Recent studies have shown that this attention based mechanism is limited in both spatial and temporal resolution (Lu and Sperling, 1996; He et al., 1996; Verstraten et al., 2000; Intriligator and Cavanagh, 2001). In contrast, low-level mechanisms can signal motion even when a stimulus is not attentively tracked and responds to motion at much higher temporal frequencies. This low-level passive system is putatively mediated by directionally selective cells in the early visual cortices (Hubel and Wiesel, 1968) and is velocity based, whereas the high-level system is position based and depends on attention (Seiffert and Cavanagh, 1998, 1999). Since parietal lesions are associated with deficits in attention, we hypothesized that parietal lesions ought to impair high-level motion perception. In the present report, we examine two high-level motion tasks, namely multiple object tracking and apparent motion. Similarities and differences in the impairments for these two high-level motion tasks should reveal similarities and differences in the attention mechanisms they may call on.

Selective attention mechanisms were tested with a task of divided attention in which the subject had to report a letter presented among three different letters for 66 or 300 ms. At the offset of the display, the subject was required to identify a letter based on its position in the letter string. The cued report for brief visual displays was first developed by Sperling (1960), and we used a modified version of his task. Recent studies have shown how patients with parietal lobe lesions can be affected in their ability to perform this type of task (Duncan et al., 1999). In contrast to the tasks of Duncan et al., we asked our subjects to report only one letter among four, and the subject never knew which letter until briefly after the letters were presented. With only four items, normal subjects could attend to and select the indicated target with ease.

Perception of motion-defined rectangles was used as a test for deficits in low-level motion perception where no tracking was involved. Subjects had to judge if the rectangles were horizontally or vertically oriented. Previous studies have shown a variety of motion deficits in patients with lesions in extrastriate motion areas, such as MT, V3, or V3A (Zihl et al., 1983; Plant and Nakayama, 1993; Vaina and Cowey, 1996; Greenlee and Smith, 1997; Vaina et al., 1998). These studies provide evidence that MT is located in the lateral temporo-occipital cortex. On the other hand, Greenlee et al. (1995) examined four parietal lobe patients and found no deficit in motion perception (speed judgments in particular). Spinelli and Zoccolotti (1992) found that the perception of moving gratings in patients with unilateral spatial neglect and parietal lesions was normal. Therefore, it appears that the temporo-occipital region, but not the parietal lobes, is involved in direction or speed judgments of low-level motion.

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One important role of attention is to select objects of interest in the environment and keep track of them as they move (Pylyshyn and Storm, 1988). A single object can be tracked with eye movements, but the eyes cannot follow more than one object; therefore, additional attentional mechanisms are required to track multiple moving objects. A typical multiple object tracking test (Pylyshyn and Storm, 1988) is constructed as follows: nine identical disks are set in random motion in a display. Four of the disks are identified as targets by flashing briefly before again becoming identical to all of the other disks. The observers keep track of the targets while all nine disks move about randomly. After 5 s, all of the items stop moving and the observer reports which disks were the four targets. With concentrated effort, most people can successfully track four targets. This task, like many video games, is engaging but tiring. Although attention is central to the performance of this task, the continuously moving disks all generate low-level motion responses as well. It is not yet clear the extent to which these low-level signals contribute to the accuracy of tracking.

Several neuroimaging and TMS studies have shown that the parietal cortex is important for visual attention in general (Corbetta et al.1993, 2000; Pascual-Leone et al., 1994; Ashbridge et al., 1997; Hilgetag et al., 2001). In addition, patient studies show that visuospatial and attentive problems are often seen after damage to the parietal lobes (Arguin et al., 1994; Robertson et al., 1997; Robertson and Manly, 1999).

A recent fMRI study (Culham et al., 1998) found that the parietal areas were significantly more active during the multiple object tracking task than in passive viewing of the same stimuli. However, tracking did not differentially activate other regions involved in motion perception (like the MT region). This lack of MT activation contrasts with prior reports of attentional modulation of low-level motion signals in this area. Thus, the results of Culham et al. (1998) would appear to be specific to high-level motion and not a general effect of attention upon motion signals (O'Craven et al., 1997). Based on these results (as would be expected), a preliminary report has found that parietal lesions disrupt attentive tracking in contralesional fields (F. Michèl et al., 1997, Cognit. Neurosci. Soc., abstract).

A stimulus does not have to move in a continuous manner to be seen to move. When a single light is flashed briefly at one location followed shortly thereafter by a second light at another location, a clear impression of motion is produced. Whether this motion is low-level or high-level and how the two separate events are linked into one motion percept (the correspondence problem) has been debated for many years (Ullman, 1978; Cavanagh and Mather, 1989).

Although the perception of motion in the flashed stimulus seems effortless, a number of studies have suggested that attention is involved (Dick et al., 1991; Verstraten et al., 2000; see Mather, 1994, for a review). Wertheimer (1912) was the first to suggest that apparent motion might involve attentive tracking: the result of the involuntary dragging of attention from the first flash to the second. Attention is "grabbed by" the first stimulus and then the second stimulus, and this is referred to as an exogenous shift of attention (Yantis, 1993) or "passive sensorial attention" (James, 1890).

Unlike attentive tracking, perceiving apparent motion seems relatively effortless. No instructions are required, and the motion percept is uniformly seen by all normal observers. It is this ease of perception, coupled with the possibility of use as a probe of attention, that has focused our interest on apparent motion as a test for patient populations. In our apparent motion task, the perception of motion depends on an accurate analysis not only of the location of the flashes but also of their timing. The evidence for a role of attention in apparent motion (Dick et al., 1991; Verstraten et al., 2000) implies that a loss of either spatial or temporal attention could disrupt motion perception. The evidence for losses in spatial attention following parietal damage is well known; additionally, there is evidence for losses in temporal attention. For example, patients affected by extensive right hemisphere lesions are impaired in auditory tasks requiring time perception (Harrington et al., 1998; Cusak et al., 2000) as well as in the orienting of attention in time (Husain et al., 1997).

One note of caution, however: if the two flashes of the apparent motion display are sufficiently close together, they will trigger both a low-level response by falling within the receptive field of a directionally selective unit and the presumed high-level response. Conversely, if the step size between the stimuli is sufficiently large (more than 2°) (Anstis, 1980), low-level motion makes no contribution to apparent motion (Anstis, 1980; Boulton and Baker, 1993).

We tested seven patients: three with unilateral right parietal lesions (cases DS, JR, and JL), three with bilateral parietal lesions (cases WGD, AT, and LF), and one control patient (case IB) with a more posterior lesion to the visual areas sparing the parietal cortex. Patients' performance was compared to three age-matched control subjects. All of our unilateral right parietal patients had some signs of visual neglect.

Results

Experiment 1: Static Letter Detection

This task measured attentional selection in the absence of any stimulus motion. We used a modified version of the partial report first used by Sperling (1960) to test selection from a brief visual display of multiple stimuli. We presented four letters in a horizontal array in one field or the other for an exposure time of 66 and 300 ms and asked subjects to report a letter from a particular position in the array, with a different position specified on each trial (Figure 1A).

Patients JR and JL were tested in this task. The results are shown in Figure 2. As expected, they both showed a selective impairment in the hemifield contralateral to the lesion site (Figure 2). Their failure to perform this task was not due to impaired visual resolution or letter recognition as the patients were both able to read these letters when presented singly.

Experiment 2: Motion-Defined Rectangles

This task examined the patients' ability to detect low-level motion. The monitor presented a field of randomly flickering black and white dots (see Experimental Procedures). In the center of one quadrant, a region of dots

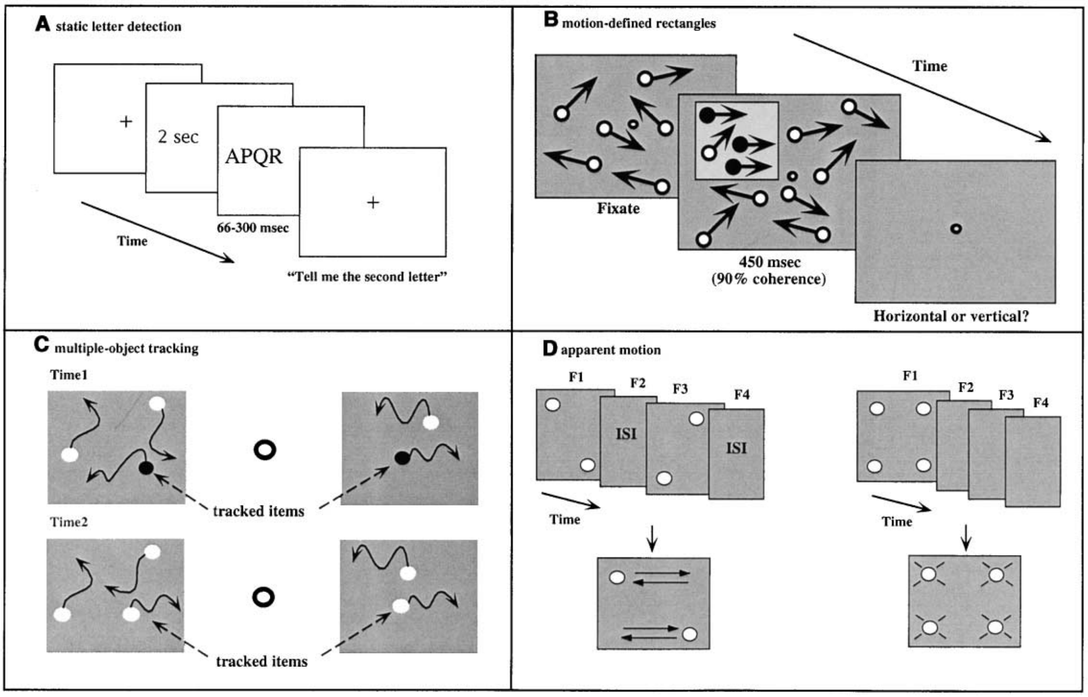

Figure 1. Examples of the Four Tasks

(A) Example of the stimuli used in experiment 1.

(B) Example of the stimuli used in experiment 2. The 90% coherence difference is shown. The arrows indicate motion, and they were not present on the display. The vertically oriented rectangle did not have a line contour as the shape was made visible solely by the difference in motion direction coherence.

(C) Example of the stimulus used in experiment 3. The subject had to track two out of five disks. In the actual task, the target disks were indicated by turning red (here depicted as black) (Time 1) for a brief interval after which they reverted to the same green as the others, while the other remained green (here depicted as white) (Time 2).

(D) Example of stimuli in experiment 4. In the apparent motion stimulus, two dots in diagonally opposite corners are flashed simultaneously and then switched off (Frame 1) and replaced by two dots appearing on the remaining two corners (Frame 2). The frames are alternated in a continuous cycle. In the flicker stimulus, all four dots are switched on simultaneously and remain on for the same duration as in the apparent motion case. At high-cycle rates, the apparent motion stimulus generates no motion impressions and appears to be four flashing dots. At these rates, the discrimination performance drops to chance.

moved together in a semicoherent fashion (Figure 1B). This coherent region was rectangular in shape and oriented either horizontally or vertically. The subject's task was to indicate the orientation. This type of test is used widely in psychophysical and neurophysiological literature to examine low-level motion mechanisms (Vaina et al., 1998; Newsome and Paré, 1988). Patients affected by MT lesions fail in low-level motion tasks where they are asked to detect motion of a small number of dots coherently moving within a dynamic background. However, they perform normally in motion segmentation tasks when the background is stationary (Vaina et al., 1990) or when there is only a low-level of background noise (Rizzo et al., 1995) at very long exposure time (5.4 s). In our task, there was always a high proportion of background noise in which the target shape was embedded, and the subjects had to detect the global motion to perceive the target shape correctly. The shape was made more visible by increasing the percentage of dots coherently moving in the same direction. Tracking the moving dots within the rectangle was not necessary to make the shape judgment, and the tracking of any individual dot did not improve the performance (the rectangular shape is a property of the overall motion, and it cannot be recovered from the motion of any individual dot). Attention is required in order to notice and report the shape of the rectangle, but the motion that defines the shape does not require attention for the shape to become visible. This has been demonstrated in a visual search task (Cavanagh et al., 1990) where the speed to

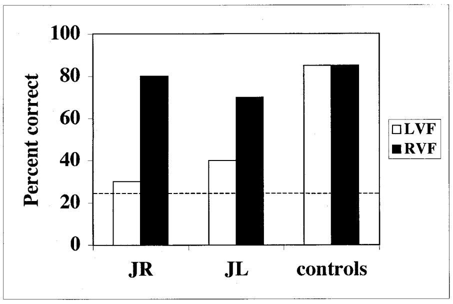

Figure 2. Static Letter Detection

The percentage of correct responses in the static letter selection task. Results for left (LVF) and right (RVF) visual fields are reported separately for patients JR, JL, and control subjects. The dotted line indicates chance (25%).

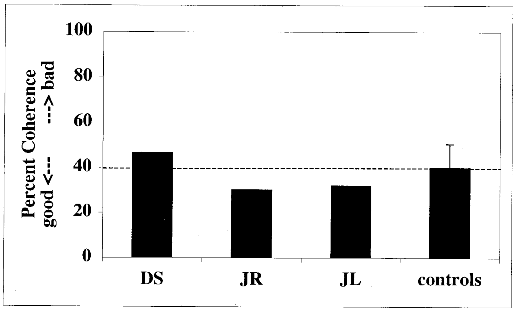

Figure 3. Motion-Defined Rectangles

The percent of dot coherence at which the subjects perform 75% correct are reported for each unilateral patient: DS, JR, and JL, and a group of three age-matched controls. Lower coherence threshold indicates better performance. Average threshold was 40 (±10.5) for age-matched control and 39.4 (±9.6) for the patients. The dotted line indicates the average performance of control subjects. On the y axis, the arrows indicate good and bad performance.

detect a vertical, motion-defined rectangle in a field of horizontal, motion-defined rectangles (distractors) was unaffected by the number of distractors.

Figure 3 depicts the results for the motion-defined rectangle judgments. The percent coherence threshold (at which the patients could report orientation at 75% correct) is shown for each patient and for age-matched controls (this threshold was obtained with a smoothed function-fitting procedure, and the function derives a point from each coherence level that is weighted by its total number of observations). There was no systematic difference in performance between the left and right visual fields. Therefore, the data in the graph for left and right visual fields have been collapsed. Thus, we confirm previous reports (Spinelli and Zoccolotti, 1992) that low-level motion perception is normal in both fields in patients with right parietal damage.

Experiment 3: Multiple Object Tracking

The next question we asked was whether the right parietal patients would also be able to perform a task that relies on the high-level (attentive) motion system. We investigated this by having the patients perform a multiple object tracking task. Subjects were asked to track either one or two items out of a field of five identical moving items. This task required continuous attentional monitoring of moving stimuli (Figure 1C). Assuming that the patients could see the low-level motion of these items, this second experiment added an attentional component of keeping track of the items as they moved.

In Figures 4A and 4B, the percentage of successful tracking responses for each visual field is reported for each patient and a group of age-matched controls. Results are reported for tracking two out of five (Figure 4A) and one out of three disks (Figure 4B). Note that when two disks had to be tracked, they were always displayed one in each hemifield. In such a situation, the best tracking strategy was to maintain fixation on the bull's-eye and follow both targets with attention. A Fisher's exact test was used to compare each hemifield of each subject with the age-matched controls. The patients could track as proficiently as the age-matched controls in their ipsilesional fields (in the portions of visual space represented in their unaffected hemisphere). However, performance in the tracking task was severely degraded in the contralesional field for the three patients. The Fisher's exact test confirmed that the contralateral fields of the patients significantly differed from the hemifields of age-matched control subjects ($p < 0.001$ for each comparison). When tracking only one disk, DS and JR showed some loss in the contralesional field (Figure 4B) but not as severe as when tracking two. JL was more severely impaired in single object tracking in the left hemifield. Because these subjects performed normally on the low-level motion task, we consider these losses a manifestation of disrupted attentional tracking rather than a loss in low-level motion processing. The partially spared ability of DS and JR to track a single moving object in the contralesional field confirmed that the stimuli were visible, their motions could be discerned, and that the task instructions were understood. With only one target on one side of fixation, there is a concern that the patients may make eye movements to bring the single target into their good field. This might also apply to the two target display, although it is less likely because if the patient had moved his eyes to the contralesional target, then he would have lost track of the ipsilesional one. Results show that this was not the case. We did ask the patients to maintain fixation, and they did not report making any eye movements to the single target. Nevertheless, some of their ability to track in the

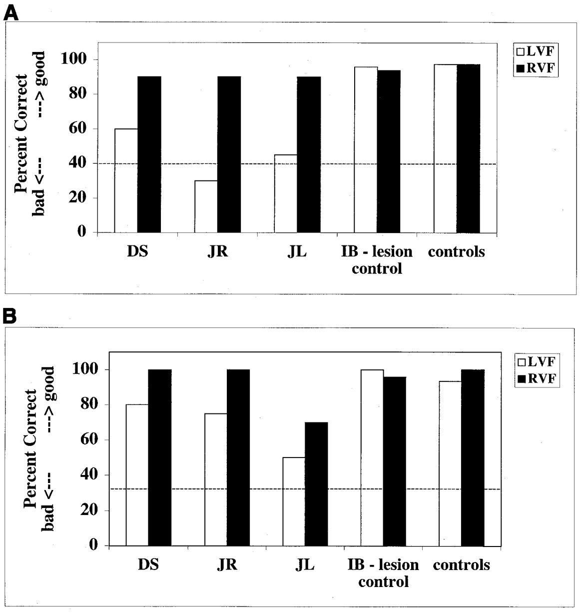

Figure 4. Multiple Object Tracking

(A) Results display tracking for two out of five disks. Percentage of correct responses are represented as a function of visual field (left and right) for each unilateral patient (DS, JR, and JL), a lesion control patient (IB), and a group of three age-matched controls. The dotted line indicates chance level (40%).

(B) Results display tracking for one out of three disks. Percentage of correct responses are represented as a function of visual field (left and right) for each patient and a group of three age-matched controls. The dotted line indicates chance level (33%). Higher percent correct indicates better performance.

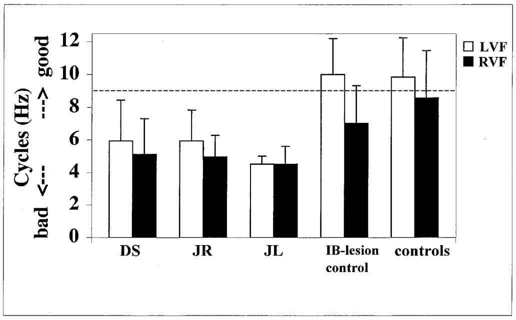

Figure 5. Apparent Motion

Motion threshold for each unilateral parietal patient (DS, JR, and JL), for the lesion control patient (IB), and three age-matched controls. The threshold is expressed as the cycle rate at which the subject could discriminate flicker from motion with 75% accuracy. The lower the threshold, the worse the performance. The dotted line indicates the average performance of the group of age-matched control subjects.

contralesional field may be attributable to uncontrolled eye movements.

On the other hand, the impairment in tracking one item in the contralesional field when there was a second target in the other field confirms the expected loss for spatial attention in the contralesional field. This result could be explained in terms of visual extinction (Vallar et al., 1994), an inability to detect a target during simultaneous presentation of another similar target in the opposite hemifield. The patients could perceive a single stimulus in either hemifield when presented alone. Extinction often persists after recovery from more severe signs of neglect (Vuilleumier and Rafal, 2000).

Experiment 4: Apparent Motion

We next asked our patients to participate in a simple apparent motion task. Subjects reported whether they saw motion or static flickering in a display of four dots. With an appropriate temporal offset between the dots, there was a compelling motion illusion (Ternus, 1938; Ramachandran and Anstis, 1983), either horizontally or vertically. In an attempt to prevent the subject from moving his/her eyes toward the target stimulus, the quadrant of presentation was unpredictable across trials. The display is schematized in Figure 1D. The frequency of alternation was varied from 1.7 to 14.9 Hz across trials. On each trial, the observers saw either an alternating quartet or a display in which all four dots appeared and disappeared simultaneously. Finally, to prevent judgements based on the first display frame (e.g., "did I just see two dots or four?"), there was a pretrial delay of 40 ms before each trial during which the four dots were flashed simultaneously.

The results are plotted in Figure 5. Note that in this task, low thresholds (slower critical rates) indicate poor performance. Motion thresholds were taken as the alternation frequency at which subjects could discriminate movement from flickering 75% of the time. The threshold was obtained by fitting the data with a smoothing function. The thresholds for both left and right hemifields are reported separately. A group of three age-matched control subjects could perceive motion at a threshold of 9.8 Hz and 8.5 Hz in the left and right visual fields, respectively, whereas all of the patients reached threshold at much lower alternation frequencies (Figure 5). Compared to the tracking task, we observed a remarkable difference in the pattern of loss (Figure 4). While object tracking was only impaired in the contralesional hemifield, all three unilateral patients (DS, JR, and JL) showed bilateral loss.

How Do Bilateral Parietal Patients Perform on High-Level Motion Tasks

We were able to test three bilateral parietal patients (LF, WGD, and AT) to see whether their deficits for apparent motion would be similar to those of the right parietal patients or more severe. They all showed selective attention impairments in both hemifields (Table 1) and bilateral losses in the apparent motion task. The patients were all able to read letters singly presented, and their linguistic abilities were preserved.

Low-level motion performance (experiment 2) was normal (patients LF and AT) or better than normal (WGD, the youngest patient). Because LF found it difficult to focus on the fixation mark, he was tested with the motion-defined stimulus at screen center, and he performed normally. Patient AT's low-level motion was tested with a slightly different task. She was presented with two squares, one with dots moving in random trajectories and another with a mixture of randomly moving dots and coherently moving dots, the proportions of which were varied. The task was a same/different judgement as a function of the coherence ratio. Her performance was in the normal range.

All three patients showed a deficit in tracking two of five items in the multiple item tracking. AT performed the visual tracking with a slightly different stimuli presentation as the target disks were displayed in one single region, whereas in all other cases, the disks were presented within two gray regions centered from fixation.

Finally, the bilateral parietal patients also showed significant losses in the apparent motion task in both fields (experiment 4). WGD did retain better sensitivity to apparent motion in his left field than in his right field. The range of thresholds for the bilateral patients was very similar to that of the right parietal patients (4–6 Hz).

Discussion

This study provides important findings about the temporal dynamics of attention in left hemispatial neglect. Patients affected by right parietal lesion are impaired at performing an apparent motion task in both left and right visual fields. Our results show that the impairment is not due to problems in low-level motion, spatial attention, selection, or tracking as all of these are at normal levels in the right (ipsilesional) field for these patients. Having ruled out these factors, we are left with only one aspect that distinguishes apparent motion from the other forms of motion that we tested: the rapid deployment of transient attention to the discrete, sequential flashes of the stimulus. We claim that the patients' difficulty with apparent motion results from the inability of transient attention to resolve the successive onsets and offsets of adjacent flashes, preventing their integration

Table 1. Bilateral Parietal Patients

Experiment	LF LVF	RVF	WGD LVF	RVF	AT LVF	RVF
Selective attention (percent correct)	20	30	30	50	N/T*	N/T
Motion-defined rectangles (**)	50.7		23.6		50	
Multiple object tracking (percent correct)	at chance	at chance	at chance	at chance	at chance	at chance
Apparent motion (Hz)	5.5	6	6.9	4.7	3.1	4

Results are reported for each bilateral parietal patient: LF, WGD, and AT.
*Not tested.
**Percent coherence averaged across hemifields (average threshold was 40 ± 10.5 for age-matched controls).
LVF, left visual field.
RVF, right visual field.

into an apparent motion percept. Moreover, the right parietal patients appear to have lost the temporal resolution of transient events in both fields. Biparietal patients show about the same loss, again in both fields, as do the patients with only right parietal lesions.

Two types of high-level motion were tested in three patients with right parietal lesions. Results from tests of attentive tracking and apparent motion revealed that a selective deficit in motion perception might be limited to high-level mechanisms, leaving low-level motion perception relatively intact. This data supports the psychophysical evidence that a low-level motion system operates independently of a higher order system that is mediated by attention (Cavanagh, 1992). The different pattern of loss in the two visual fields also suggests that the attentional resources responsible for the perception of apparent motion differ from those required in attentive tracking.

Results from experiment 1 (selective spatial attention) confirmed the attentional deficit resulting from parietal damage in the two patients tested (JR and JL). Results from experiment 2 (motion-defined shapes) showed that all patients were able to detect low-level motion as proficiently as normal controls. In experiment 3, two of the right parietal patients could perform the multiple object tracking task when they had to track only one item out of three in their left visual field. Thus, these subjects could perceive and track continuous motion in the contralesional field if the attentional load was not too great. None of the right parietal patients were able to keep track of the target in the contralesional field when one target had to be tracked in each hemifield but could keep track of the target in the ipsilesional field. Despite intact low-level motion perception, one subject was impaired at tracking even a single moving object in the left hemifield (with no target on the right hemifield), indicating a more severe problem with attentional tracking.

In addition to the expected loss of tracking performance, the patients also showed significant losses in the apparent motion task in experiment 4. Surprisingly, the three patients also showed a substantial impairment for tests in the ipsilesional field where attentive tracking had shown no loss. This bilateral loss might indicate a generalized timing deficit (Husain et al., 1997). If the timing of the dot onsets and offsets is poorly registered, they may appear to be overlapping in time rather than alternating. The perception of apparent motion deteriorates significantly for overlapping presentations of the two stimuli. Timing deficits may not be important for attentional tracking where the stimuli are continuously present.

Whatever the case, we find that across patients and visual fields the pattern of loss for apparent motion is not the same as that for attentive tracking, suggesting that the underlying cause, although quite plausibly related to attention in both cases, is different. We mentioned previously that the tracking task requires voluntary attention to the targets whereas the apparent motion display draws involuntary attention to the stimu-

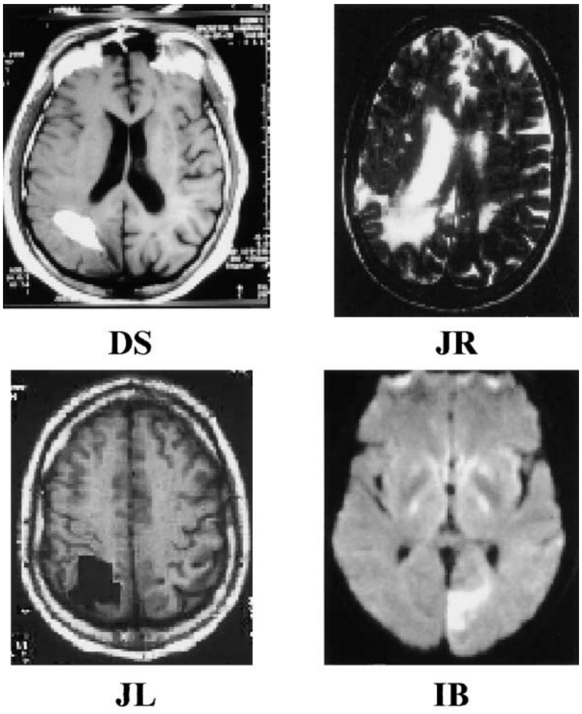

Figure 6. Brain Images of Unilateral Lesion Patients

Horizontal MRI sections through the cerebral hemispheres of four patients with unilateral lesions (DS, JL, JR, and IB) are shown here. The left side of each image represents the right hemisphere (neuroradiological conventions).

Table 2. Distribution of Lesions

Patient	Superior Parietal Lobule	Angular Gyrus	Supramarginal Gyrus	Precuneus	Lateral Occipital Gyri	Cuneus	Lingual Gyrus	Middle Temporal Gyrus	Inferior Temporal Gyrus
DS	R	R	R	R					
JR	R	R	R	R	R			R	
JL	R	R	R	R	R	R			
IB	L			L		L	L		
LF	R,L	R,L	R,L		R,L			R	
WGD		R,L			R,L			R	R
AT	R,L	R,L	R,L		R,L	L			

Distribution of lesions involving visual cortex and multimodal cortex in the parietal, occipital, and temporal lobes.
R, right hemisphere.
L, left hemisphere.

lus. Thus, one possible explanation of the dissociation in outcomes for the two tasks is that it reflects variations in the contributions of the two hemispheres to endogenous and exogenous attention (Corbetta et al., 2000). In an fMRI study, Corbetta and coworkers found that the temporo-parietal junction and the precuneus in the right hemisphere were active when a visual target appeared at an unattended location, while both intraparietal sulci were active during voluntary orienting to a target. Although the size of the lesion varies across our right patients (Figure 6), they all had lesions involving the angular gyrus (which includes the area called the temporo-parietal junction by Corbetta et al.) and precuneus (see Table 2 for a synthesis of the anatomical distribution of the lesion for each patient) which Corbetta et al. implicate in the orientation of attention toward sudden stimuli in an unattended area like those in our apparent motion task. Alternatively, a combined PET and fMRI study (Coull and Nobre, 1998) showed activation of the right parietal cortex when subjects were required to attend to both spatial and temporal properties of a cue. Our apparent motion task requires orienting of attention in space to sudden onsets together with a precise registration of temporal intervals within the target stimulus. Hence, it may be the conjunction of both spatial and temporal attention that creates the right hemispheric bias in our apparent motion task.

Interestingly, a recent single unit study in macaque monkeys (J. Assad, personal communication) supports our findings. Direction-selective neurons in parietal cortex were tested with a visual stimulus consisting of evenly spaced columns of dots that could be displaced at fixed intervals by a fraction of the intercolumn spacing to create a uniform apparent motion. The animals were trained to report the direction of the apparent motion. On some presentations, the dots were displaced by exactly half of their intercolumn spacing such that the perceived direction of motion was perceptually bistable. On these bistable presentations, many neurons in the lateral intraparietal area (LIP) were more active when the animal reported perceiving the neuron's preferred direction of motion than the opposite direction of motion. In MT and MST, far fewer neurons were modulated by the animal's report of direction on perceptually bistable trials. Therefore, higher parietal cortical areas appear to be somehow involved in a representation that reflects subjective perception.

Finally, it is interesting to notice that all three right

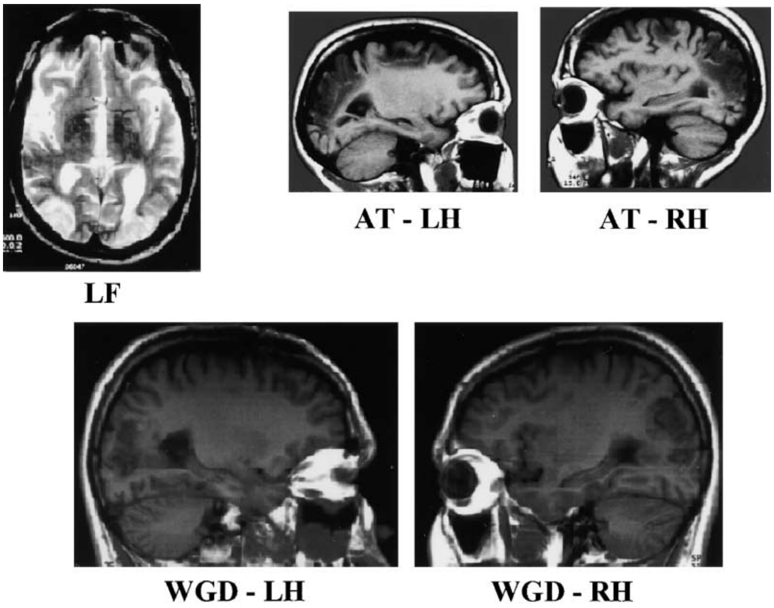
LF
AT - LH
AT - RH
WGD - LH
WGD - RH

Figure 7. Brain Images of Bilateral Patients

Horizontal and sagittal MRI sections through the cerebral hemispheres of patients with bilateral lesions (LF, WGD, and AT) are shown here, showing their left (LH) and right (RH) hemispheres.

parietal patients lost the perception of apparent motion at alternation rates higher than 6 Hz, which corresponds to an SOA of about 200 ms. This is similar to the results reported by Rorden et al. (1997), where the authors presented right parietal patients with a temporal order judgement (TOJ) task. They presented two unconnected bars, one in each visual field with different time intervals between them, and the patients were asked to report which bar appeared first. The authors assumed that when two stimuli were physically simultaneous, the bar that had the subject's attention would be seen first. When normal subjects were asked to maintain fixation, they correctly reported simultaneous stimuli as simultaneous. In contrast, Rorden et al. needed to present the contralesional bar 200 ms in advance in order for the parietal patients to judge it as simultaneous with the bar in the ipsilesional field. With anything less than 200 ms advanced presentation, the patients always judged the ipsilesional bar as coming first. They explained the results in terms of a disruption in the ability to judge the order of events displaced in space (one in each hemifield) and time. This impairment causes a severe bias to the right (ipsilesional side) and a consequent delay in visual awareness for contralesional events. We demonstrated that a timing deficit can occur within each field, a result that rules out a simple differential delay between the two hemifields or an alertness problem (Robertson et al., 1998) as the only underlying cause of the deficit in the apparent motion task.

Furthermore, although our patients could all discriminate synchronous from alternating flashing at rates in the range of 2–4 Hz, performance abruptly fell to chance again at lower rates for some of them. These results contrast sharply with those found with normal observers who can see motion up to SOAs of 700 ms (1.4 Hz). Patient IB, who had a left occipital lesion, performed the task as well as age-matched controls in all conditions.

In sum, we found that right parietal lesions can cause a visual tracking deficit in the contralesional field, while performance in the ipsilesional field remains intact. Furthermore, we found that apparent motion can also be disrupted by right parietal lesions, whereas the perception of low-level motion remains intact. Performance of our parietal patients in this task was different from that of the patients affected by lesion to the motion area MT (Vaina et al., 1990; Rizzo et al., 1995). Furthermore, the features of our low-level motion task ruled out the possibility that we were testing independent motion processing areas such as KO (Dupont et al., 1997) or early visual areas such as V1, which has been demonstrated to be significantly active during motion segmentation tasks (Reppas et al., 1997). In our task, the percentage of dots coherently moving in the same direction in the target shape varies randomly across trials between six levels (see Experimental Procedures for more details), while in the tasks used in the fMRI studies mentioned above the dots density was constant. In a coherence motion task (similar to our low-level motion task) used in a recent fMRI study (Shulman et al., 1999), patterns of strong activation were observed in MT. This data supports our finding that visual areas subserving low-level motion were preserved in our patients.

Finally, the different attentional deficits we found in our patients could indicate a more general spatial and temporal resolution deficit of visual perception which could probably affect other modalities. A recent study (Harrington et al., 1998) confirms this hypothesis and supports the idea of a role of the right inferior parietal cortex in time perception task with auditory stimuli. Right parietal patients were unable to judge the difference in duration of two tone pairs, while left parietal patients could perform the task as well as normal controls.

The data collected with bilateral parietal patients (see Table 1 and Figure 7) shows that, as expected, performance on the selective attention, tracking, and apparent motion tasks was poor in both fields, whereas low-level motion was preserved in both fields. Most importantly, for the apparent motion task, the loss in performance was no worse than for the patients with only right parietal lesions. We are currently investigating left parietal patients to determine whether the bilateral deficit we found is specific to the right parietal patients. We ran three unilateral left parietal patients, and preliminary data showed preserved ability to perform low-level motion perception. In the attention-based motion tasks, two patients were impaired at tracking the disks in the field contralateral to the lesion (right visual field) confirming the attentional deficit while the third patient performed like normal controls in this task. Furthermore, two of the left parietal patients performed normally in the apparent motion task, while one showed losses, more severely in the left visual field. This last patient had additional lesions in the right basal ganglia that might have contributed separately to a deficit in visual spatial attention (Vallar, 1993; Bellmann et al., 2001).

In conclusion, our data support two different roles for attention in high-level motion, and these are affected differently by parietal lesions. Active tracking tasks appear to call on voluntary, sustained attention, and this is impaired in the field contralateral to the lesion. Apparent motion tasks appear to rely on involuntary, transient attention, and the resolution of events picked up by this attention system appears to be much reduced following right parietal damage. This loss then degrades apparent motion performance in both fields.

Experimental Procedures

Case Histories

We formally tested seven stroke patients. Three of the patients, DS, JR, and JL had unilateral, right parietal lobe lesions with some extension into surrounding structures. Three of the other patients, WGD, LF, and AT, had bilateral lesions involving parietal cortex and surrounding structures. In one patient, IB, the lesion principally involved the left occipital cortex with limited extension into adjacent parietal cortex. Magnetic resonance images (MRIs) acquired for clinical indications were analyzed to define the anatomical distribution of the lesions using the Damasio atlas (1995). Three subjects, two males and one female, with no history of neurological disease (mean age 65.6), served as age-matched normal controls.

Patient DS, a 65-year-old right-handed man, was admitted to the hospital in September 1998 with left hemispatial neglect and mild left hemiparesis. Computerized tomography (CT) showed a hemorrhage involving deep and superficial right parietal lobe structures. Two months later, MRI showed signal abnormalities involving the right superior parietal lobule, angular gyrus, supramarginal gyrus, and precuneus (Figure 6). When we first tested DS 6 months after his stroke, he felt fully recovered and was back to his usual activities, including golf. However, he complained that he consistently drove the ball off to the right of the fairway. On the Sunnybrook neglect battery (Black et al., 1990), DS scored 14/100, indicating mild residual left hemispatial neglect.

Patient JR, a 70-year-old right-handed man, was admitted to the hospital in October 1998 with left hemispatial neglect, left superior quadrantanopia, normal visual acuity, and left hemiparesis. CT revealed a hemorrhage involving deep and superficial right parietal lobe and temporal lobe structures. Ten months later, MRI showed extensive signal abnormalities involving the right superior parietal lobule, angular gyrus, supramarginal gyrus, precuneus, lateral occipital gyri, and middle temporal and superior temporal gyri. The anterior extent of the lesion also involved the transverse gyrus of Heschl, parahippocampal gyrus, temporal pole, postcentral and precentral gyri, and the inferior frontal gyrus. Deeper involvement included the insula, putamen, and posterior limb of the internal capsule (Figure 6). We first tested JR 8 months after his stroke. He complained of strange visual phenomena, such as an ant changing location on the floor without actually having seen it move from one position to another. On the Sunnybrook neglect battery (Black et al., 1990), JR scored 10/100, indicating mild residual left hemispatial neglect.

Patient JL, a 62-year-old right-handed man, suffered a left occipital lobe hemorrhage in 1998 and a right parietal hemorrhage in 1999. After the first stroke, the patient exhibited symptoms of right hemianopia, which gradually recovered. After the second stroke, the patient exhibited symptoms of left hemianopia, which have not improved. Nine months after his second stroke, MRI revealed right-sided signal abnormalities involving the superior parietal lobule, angular gyrus, supramarginal gyrus, precuneus, cuneus, and lateral occipital gyri (Figure 6). There was no imaging evidence of his prior left-sided lesion. A clinically occult lacunar infarct was also seen in the left pons. We first tested JL 11 months after his second stroke. He complained that his vision looked "watery" and that stationary visual objects were jumping and moving. Examination revealed a left inferior quadrantopia. Visual acuity with correction was 20/40 in his right eye and 20/25 in his left eye. On the Sunnybrook neglect battery (Black et al., 1990), JL scored 40/100, indicating severe left hemispatial neglect.

Patient IB, a 70-year-old right-handed man, was admitted to the hospital in 1998 with a right homonymous hemianopia. MRI on admission revealed ischemic infarction of the left cuneus, lingual gyrus, and underlying white matter with extension into small portions of the superior parietal lobule and precuneus (Figure 6). When we tested IB 6 months later, his visual fields were full and his performance on the Sunnybrook neglect battery (2/100) was normal.

Patient LF, a 73-year-old man, was admitted to the hospital in 1999 with Bálint's syndrome (simultanagnosia, oculomotor apraxia, and optic ataxia). MRI revealed ischemic infarcts involving the right and left superior parietal lobule, angular gyrus, supramarginal gyrus, and lateral occipital gyri plus the right middle temporal gyrus, left postcentral gyrus, and left precentral gyrus (Figure 7). When we tested LF 5 months later, he complained of "scrambled vision." He misreached for objects, had difficulty locating leftward and rightward targets on a figure-cancellation task, copied only fragments of drawings (e.g., the petals of a daisy without the leaves, stem, and pot), and had difficulty reading because words appeared fragmented. Goldmann perimetry disclosed bilateral inferior visual field defects that were worse on the left, and his visual acuity was 20/30 using the right eye and 20/70 using the left eye. On the Sunnybrook test battery, he omitted items on both sides of space, without a lateralized bias.

WGD, a 22-year-old right-handed man, was admitted to the hospital in November 1998 with a headache, Bálint's syndrome, and left face and hand numbness. MRI revealed ischemic infarction of the right and left superior parietal lobule, angular gyrus, and lateral occipital gyri plus the right middle and inferior temporal gyri (Figure 7). When we first tested him 6 months after his strokes, WGD's Bálint's syndrome was much improved; there was a left inferior quadrantopia, normal visual acuity, and no evidence of hemispatial neglect (5/100 on Sunnybrook test battery). WGD reported difficulty playing video games and following action sequences in movies (e.g., sword fights) because they appeared fragmented.

Patient AT, a 45-year-old woman, was admitted to the hospital with eclampsia and hemorrhages into the parietal and occipital lobes bilaterally (Figure 7). MRI showed signal abnormalities in the right and left superior parietal lobule, angular gyrus, supramarginal gyrus, lateral occipital gyri, and postcentral gyrus plus the left cuneus. When we tested AT 15 years later, signs of Bálint's syndrome were still present. Visual field testing revealed homonymous paracentral scotomas in the right inferior quadrant.

Table 2 reports a synthesis of the anatomical distribution of the lesion for each patient.

Ethical committee approval from Harvard University and from Beth Israel Deaconess Medical Center were granted for all procedures.

Equipment

The experiments were conducted on a PowerMac 120 computer. Software for experiments 2, 3, and 4 were written in Think C using programming routines (Shell) created by Raynald Comtois (http://www.kagi.com/visionshell/). Experiment 1 was programmed on PsychLab 2.2.6 for Macintosh. An Apple Hi-Res color monitor was used for all experiments for all subjects except JR, JL, and LF, where a Powerbook 1400c/166 computer and Apple Studio Display were used. The monitors were calibrated for linearity before the experiments were conducted. The same basic equipment was used in all experiments.

Stimuli and Procedure

In experiments 2 and 4, the stimuli were always presented centered 10° from the fixation point in one of the four quadrants: upper left, upper right, lower left, or lower right. The presentation of the stimuli was in one of the four quadrants randomly across trials. We emphasized to the observers that because the stimulus position was uncertain, it was important for them to maintain fixation. There were equal numbers of presentations in each of the four quadrants, and stimulus conditions were selected such that there were equal numbers of each. All experiments were conducted in a dimly lit room at 57 cm viewing distance from the display. When the subject presented a field defect diagnosed with the neuro-opthalmological exam, the experiment was modified in order to avoid testing the impaired portions of the visual field. The subject's vocal response was entered by the experimenter on the keyboard.

Experiment 1: Static Letter Detection

We used a letter detection task in which four black letters were presented to either the left or right of a fixation cross placed in the center of an all white background. On each trial, the four letters were centered 2° from fixation, were written in uppercase, and had no meaning (i.e., they were not words). Each letter subtended $1° \times 1°$ of visual angle (Figure 1A). They were presented for 66 or 300 ms, and no masking was used. The following procedure was used: the fixation cross was presented for unlimited time until the space bar was pressed (to make sure that the patient was correctly fixating before each trial). After 2 s, the four letters were presented, and immediately after each trial the experimenter instructed the subject to name one of the four letters (e.g.: "tell me the third letter" or "tell me the first letter"). The percentage of correct responses was measured as a function of the side of presentation (left or right). The experiment consisted of 20 trials, ten for each side of presentation, randomly distributed across trials. Before beginning the experiment, six practice trials were run.

Experiment 2: Motion-Defined Rectangles

In this task, we measured the ability of the subject to perceive two-dimensional shapes generated by a difference in motion coherence of the target dots compared to the background (Figure 1B). The background consisted of randomly moving black and white pixel dots of 50% density and a mean luminance of 60 cd/m^2. The dots moved at a velocity of 3°/s. On each trial, the subject had to identify the orientation of a rectangle (subtending $7.5° \times 4.3°$) presented for 450 ms in one of the four quadrants randomly across trials. The rectangle could be oriented either horizontally or vertically (a two-alternative forced choice procedure). The difference (the percentage of dots coherently moving in the same direction) between the shape and the background was varied randomly across trials. The percentage of coherence differences tested were: 20%, 35%, 50%, 65%, 80%, and 95%. The stimuli were presented in blocks of 96 trials for each visual quadrant (16 trials for each level of coherence, for a total of 384 trials) randomly ordered, with 15 practice trials preceding the beginning of the experiment.

Experiment 3: Multiple Object Tracking

To ensure that the observers maintained fixation during tracking, two gray regions on a black background were simultaneously present on the screen during each trial, each one centered 4.5° from fixation in the right and left visual fields, respectively. The two gray regions consisted of two squares 3.5 cm per side. Within the regions, five identical green (20 cd/m^2) disks (0.5 cm diameter) moved in a semirandom fashion. The velocity of the disks was 2°/s (Figure 1C). Although all motions were approximately linear, very small random variations in the path of each disk were introduced every 45 ms producing unpredictable paths. These disks "bounced" off the edge of the square and repelled one another, never colliding or occluding one another. During each trial, one or two of the disks were changed to red for 1.2 s (or more if necessary for the patient) and then turned back to green. The observer's task was to keep track of the disks while keeping the gaze steady on a bull's-eye which appeared in the center of the display to provide a fixation point. After 5 s, all five disks stopped moving, and the observer indicated (via a mouse) which one (or two disks) was the one that had turned red at the beginning. The target to be tracked could have been presented as follows: (1) one target disk presented in the left or right of the visual field among four distractors, two for each side, or (2) two target disks which could be one on the left and one on the right visual field, with the remaining three distractors distributed between the two hemifields. The stimuli were presented in blocks of 20 trials for each condition (one disk or two disks) for a total of 40 trials, randomly ordered, with ten practice trials preceding the beginning of the experiment. Before each trial, the experimenter checked the observer's eye position visually to make sure he/she was always fixating the bull's-eye.

Experiment 4: Apparent Motion

We used a variant of the simple (two dots) apparent motion display called the "quartet display" (Ternus, 1938). This display involved the alternation of two visual frames. On the first frame, two white dots (each measuring 0.5° in diameter) were arrayed on diagonally opposed vertices of a square (measuring 2 × 2 cm), and on the next frame the dots were arrayed on the opposite pair of vertices (Figure 1D). If the interval between the successive frames was appropriate, observers perceived apparent motion of two dots in either a horizontal or vertical direction. The frequency of alternation was varied from 1.7–14.9 Hz across trials. The disks were white (luminance of 70 cd/m^2 on a gray background, with a mean luminance of 25 cd/m^2). Before each trial, there was a pretrial delay of 40 ms, during which the four dots were flashed simultaneously. This was done in order to prevent the observer from giving a response based only on the cue given by the first frame (two dots in case of motion or four in case of flashing). The aspect ratio of the imaginary square upon which the dots were placed was equal to one.

For the comparison stimulus, four dots were presented in synchrony with equivalent timing.

Within a two-alternative forced choice procedure, the observer had to report whether he or she saw two moving or four flashing dots. Percentage of correct responses was measured as a function of the cycle rate. At all cycle rates, each dot was present for 25% of the overall cycle duration (25% duty cycle). At very rapid rates the subjects could not distinguish between flashing and moving dots, whereas at slower rates the apparent motion was not visible any longer, and subjects reported alternation of the dots instead of motion. A threshold-to-motion perception was calculated which corresponded to 75% of correct responses. Exposure time for each trial was set at 500 ms. The stimuli were presented in blocks of 32 trials for each SOA level (eight levels: 14.9 Hz, 9.7 Hz, 6.3 Hz, 4.1 Hz, 3.1 Hz, 2.5 Hz, 2.1 Hz, and 1.7 Hz), and each visual quadrant was randomly ordered. Each subject ran a total of 1024 trials. Before the beginning of the experiment, we gave each of the subjects examples of flashing and moving dots, changing the cycle rate manually from very rapid (30 Hz) to very slow (2 Hz) in order to familiarize subjects with the task and to test whether they could see any motion at all. Ten practice trials were also run preceding the beginning of the experiment.

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