

Neuronal representation of occluded objects in the human brain

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Abstract

Occluding surfaces frequently obstruct the object of interest yet are easily dealt with by the visual system. Here, we test whether neural areas known to participate in motion perception and eye movements are regions that also process occluded motion. Functional magnetic resonance imaging (fMRI) was used to assess brain activation while subjects watched a moving ball become occluded. Areas activated during occluded motion included the intraparietal sulcus (IPS) as well as middle temporal (MT) regions analogous to monkey MT/MST. A second experiment showed that these results were not due to motor activity. These findings suggest that human cortical regions involved in perceiving occluded motion are similar to regions that process real motion and regions responsible for eye movements. The intraparietal sulcus may be involved in predicting the location of an unseen target for future hand or eye movements.

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1. Introduction

How does the brain process a moving object when it passes behind an occluding surface? This question highlights a dissociation that is pervasive in normal behavior: the dissociation between what we see and what we know (Albright, 1995).

The dissociation between what we see and what we know has been used as a tool to study the beliefs infants hold about the world. Piaget (1954) proposed that young infants do not believe that an object continues to exist when it becomes occluded. However, recent studies suggest that infants as young as 4 months believe that objects continue to exist when they undergo occlusion (Baillargeon, 1986, 1987).

Vision researchers have noted that the completion of objects behind occluding surfaces is an everyday visual problem and that it is possible that the visual system has evolved to solve the problems posed by occluding surfaces. This idea is supported by data from psychophysical studies of occlusion that suggest that occluding surfaces are resolved early in vision, independent of our knowledge about familiar objects (Shimojo & Nakayama, 1990).

More evidence in support of this idea is offered by neurophysiology studies. Assad and Maunsell (1995) recorded from cells in monkey intraparietal sulcus (IPS) while the monkeys made movements to the extrapolated position of occluded moving targets. The IPS is located in the dorsal visual stream and is involved in high-level motion perception. The results showed that activity was present in motion-sensitive neurons in posterior parietal cortex during the inferred motion condition but not during the inferred static condition. The authors suggest that the activity reflects a general representation of motion or target position (also see Eskander & Assad, 1999).

The IPS and the superior parietal lobe are good candidates for regions that process occluded motion. Areas in and around the IPS have been implicated in high-level motion perception (Bremmer et al., 2001), visually guided movements (Andersen & Gnadt, 1989), and attention (Rushworth, Paus, & Sipila, 2001).

The middle temporal (MT) area and the middle superior temporal (MST) area may also be involved in processing occluded motion. Cells in these areas respond to direction of simple motion (Maunsell & Van Essen, 1983), and to simple and complex optic flow pattern (Duffy & Wurtz, 1991), and to other types of complex motion patterns. Functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) studies have shown that a similar area is responsive to visual motion in humans (Beauchamp, Cox, & DeYoe, 1997; Cheng, Fujita, Kanno, Miura, &

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Tanaka, 1995; Cornette et al., 1998a,b; Dupont et al., 1997; Dupont, Orban, De Bruyn, Verbruggen, & Mortelmans, 1994; Lewis, Beauchamp, & DeYoe, 2000; McCarthy et al., 1995; O'Craven, Rosen, Kwong, Treisman, & Savoy, 1997; Paradis et al., 2000; Smith, Greenlee, Singh, Kraemer, & Hennig, 1998; Sunaert, Van Hecke, Marchal, & Orban, 1999; Tootell et al., 1995; Watson et al., 1993; Zeki, 1972). This motion-sensitive region has been agreed to be homologous to macaque MT on the basis of its responsiveness to motion, not on grounds of its anatomical location.

In this study, we investigate human neural areas involved in the perception of occluded motion. A pilot study ran subjects in an occlusion task and found that one region that differentially processed occluded motion as compared to motion that simply stopped was the IPS. Less robust activations were found in the human analogue of MT/MST. The results from the pilot study were used to hypothesize activations likely to be found in Experiments 1 and 2. Thus, we concentrated on the IPS and MT/MST as regions of interest. The IPS activation may correspond to the region that responded to occluded motion reported by Assad and Maunsell (1995).

2. Experiment 1

2.1. Methods

2.1.1. Subjects

Nine volunteers participated in Experiment 1. They ranged in age from 18 to 41 years. All of the subjects gave informed consent to a protocol reviewed and approved by the Human Investigation Subject Committee of the School of Medicine at Yale University. None had previous or present history of medical illness, and all subjects were right-handed.

2.1.2. Stimuli

There were two types of stimuli used: (1) *Main Experimental Stimuli*; and (2) *Localizer Stimuli*. The Localizer Stimuli were used to localize smooth pursuit eye movement and motion perception regions in each participant. These regions were later used in the region of interest (ROI) analysis. The localizer task was run and analyzed separately from the rest of the experiment.

2.1.2.1. Main Experimental Stimuli. Sequences of MR images were acquired during six runs of the Main Experimental Stimuli. There were three different pseudo-randomly interleaved conditions: occluded motion (Occlude), disappearing motion (Disappear), or no motion (Static). Subjects had no way of knowing which condition was next. All conditions were presented with no ISI. Each condition was presented eight times and each condition lasted 12 s.

The stimuli in the *Occlude* condition consisted of 12 s movies of a small gray-and-white ball moving across a light

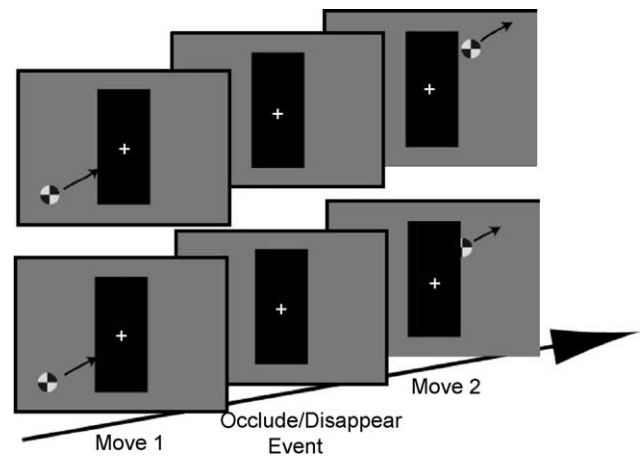


Fig. 1. A schematic illustration of the experimental task. The top panel illustrates the Disappear condition. The ball moved towards the occluder, bumped into it, and disappeared. After a short duration, the ball reappeared on the other side of the occluder. The bottom panel illustrates the Occlude condition. The ball moved towards the occluder and smoothly passed behind it. After a short duration the ball reappeared on the other side of the occluder.

gray screen. In the center of the screen was a black rectangular occluding block with a white fixation cross. The ball moved continuously as it slowly became completely occluded by the black block and then slowly re-emerged on the opposite side and continued its trajectory across the screen (Fig. 1). Each part of the movie, the initial movement, the occluding event, and the end movement lasted 4 s.

The stimuli in the *Disappear* condition consisted of an identical 12 s movie except that the small ball did not pass behind the occluder. Instead, the ball moved up to the occluder, paused at contact, and abruptly disappeared. There was no ball or motion for 4 s. The ball abruptly re-appeared on the opposite side of the screen in a position near the block (and in a position that was likely, given the ball's earlier trajectory), and then moved back along the trajectory in which it had previously been moving (Fig. 1).

Motion velocity and timing were the same in both conditions. Six different motion trajectories were used in these conditions. The entire stimulus, including the background, ball, and occluder, subtended approximately 20° of visual angle.

In the *Static* condition, subjects viewed the same stimuli as in the *Occlude* and *Disappear* conditions except that there was no ball stimulus, and thus no movement. Subjects simply fixated on the white central cross.

2.1.2.2. Localizer Stimuli—IPS. The Localizer Stimuli consisted of two interleaved conditions: a moving ball (Eye Move condition), or fixation. Conditions were presented back-to-back with no intervening stimuli or pauses.

The Eye Move condition was 12 s long and was presented nine times. In the Eye Move condition, subjects tracked a small ball as it moved across the screen. Instead of moving behind a large black occluder, it moved in front of the

occluder. Other aspects of the stimuli—size, background color, etc.—are the same as in the Main Experiment Stimuli.

The Fixation condition was 18 s long and was presented 10 times. In the Fixation condition, subjects viewed the same stimuli except that there was no ball and no motion. In both conditions, a small white fixation cross was superimposed on top of the black occluder. The last three subjects of Experiment 1 were run in a localizer task that had the same Eye Move condition, but a different Fixation condition. Their Fixation condition contained the same black occluder with a *static* ball that was on different sides of the occluder on different trials. A small white fixation cross was superimposed on top of the black occluder.

2.1.2.3. Localizer Stimuli—MT/MST. A pilot experiment ($N = 8$ subjects) localized a region suggested to be MT/MST using moving ring stimuli, similar to those used in previous studies to localize the human homologue of MT (Lewis et al., 2000; Puce, Allison, Bentin, Gore, & McCarthy, 1998; Tootell et al., 1995). The Localizer Stimuli consisted of two interleaved conditions: outward moving low-contrast concentric rings or static concentric rings. Moving stimuli were compared to the static condition in which a single frame of rings was continuously present. Stimuli were black and white, on a black background. Conditions were presented back-to-back with no intervening stimuli or pauses. Each moving ring sequence was 12 s long and was presented nine times. Each static ring condition was 18 s long and was presented 10 times. Subjects were instructed to maintain fixation on the center of the rings. The entire stimulus subtended approximately 20° of visual angle.

2.1.3. Task

Prior to scanning subjects were given a practice session to ensure that they could comply with all eye movement/fixation instructions. They were shown sample stimuli to ensure that differences between conditions were apparent to all subjects.

Subjects passively viewed stimuli in the localizer task. They were instructed to maintain central fixation and refrain from moving their eyes in the Fixation condition, but were told to follow the ball with their eyes in the Eye Move condition.

In the Main Experimental task, subjects were trained to attend to the moving ball without making eye movements (see Culham et al., 1998). They were instructed to press a button when the ball appeared on the side of the screen opposite from which it had started. They pressed the key at any time during the Static condition. It was emphasized that central fixation was critical, and subjects were reminded of this between each run of the experiment. To test compliance with instructions, eye movements were assessed in two subjects outside of the magnet under free eye movement

conditions (e.g. Eye Move condition) and under Fixation conditions (e.g. Occlude and Disappear conditions).

2.1.4. Apparatus

Moving stimuli were Quicktime movies that used static images generated by MATLAB (MathWorks, MA). Stimuli were presented from a Macintosh computer using Psycscope software (Cohen, MacWhinney, Flatt, & Provost, 1993). Stimuli were projected via an LCD projector onto a screen located at the base of the scanner bed that was viewed through a mirror angled above the participant's head.

2.1.5. Eye movement recording

Eye movements were recorded in two subjects using an infrared monitoring system (ISCAN, Burlington, MA). Eye movements in the horizontal and vertical planes were obtained during free viewing and Fixation conditions during the course of a 12 s movie.

2.1.6. Imaging and image analysis

2.1.6.1. Scanning procedure. MRI scans were acquired using a 1.5 T General Electric Signa LX scanner. Subjects' heads were restrained within a circularly polarized head coil. Anatomical images in the sagittal and coronal planes (TR = 500 ms; TE = 14 ms; sagittal: 22 slices, 5 mm thick, 256×192 matrix, FOV = 24 cm; coronal: 9 slices, 7 mm thick, 256×192 matrix, FOV = 20 cm \times 20 cm) were acquired to aid in normalization of individual participant data into standard stereotactic space (Talairach & Tournoux, 1988).

Functional images were acquired using echo planar imaging (gradient echo single shot sequence, 304 images per slice, which includes the dead time at the beginning of each run, FOV = 20 cm \times 20 cm, matrix = 64×64 , NEX = 1, TR = 1000 ms, TE = 60 ms, flip angle = 60°). This TE was chosen because several studies have shown that the $T2^*$ of gray matter is approximately 60 ms at 1.5 T (C. Gatenby, unpublished data). A rapid TR was used to maximize data acquisition during the occlusion event. Nine 7-mm-thick coronal slices, (gap interval = 1 mm), aligned perpendicular to the AC-PC line, covered visual cortex and much of the parietal and posterior temporal cortices. Images obtained at the beginning of the Localizer and Main Experimental Sessions were discarded to ensure magnetic equilibrium.

2.1.6.2. Data analysis. Images were corrected for artifacts and motion. Data analysis was performed using SPM for motion correction and software written in MATLAB that is similar to other standard image-analysis software (Skudlarski, Constable, & Gore, 1999). Maps of percent signal change were created with a hemodynamic response delay function of 3 s. The individual maps were transformed into standardized Talairach atlas coordinates (Talairach & Tournoux, 1988). Data from the localizer task were analyzed as a block-design.

Data from the Main Experimental task were analyzed as a mixed-design experiment where each task component was treated as a separate event.

The standardized statistical maps were used in linear contrasts, which represent mean activation levels between one condition and another condition. The t -statistics were computed and used to derive a measure of the signal change at each voxel relative to its own intrinsic noise variability. Next a standard linear contrast was computed for each complex effect. This procedure generates a single value for each voxel that was determined by the weighted comparison of one (or more) tasks against another set of tasks. Under the null hypothesis of no effect, the expected value of this contrast is equal to zero. The extent to which the contrast value reliably deviates from zero is then assessed. Significance levels were assessed using a skewed t -test.

2.1.6.3. Data analysis—region of interest analysis. ROIs were defined functionally by drawing regions around the two activations from the localizer task: MT/MST and posterior parietal cortex. The MT/MST ROI was in the vicinity of the ascending limb of the inferior temporal sulcus. The parietal ROI was in the region of the superior parietal lobe and the intraparietal sulcus. ROI analyses do not have the problem of multiple comparisons and as such P -values are uncorrected.

2.2. Results

The percept of occlusion was compelling for all subjects. All subjects reported that they perceived a moving ball become occluded and then reappear in the occlusion condition. In contrast, the disappear condition was perceived as a moving ball “blinking” out of existence and then reappearing.

2.2.1. Eye movements

Eye movements were analyzed in two subjects outside of the magnet using an eye tracker. Subjects watched the same stimuli used the localizer task, and in the Occlude and Disappear conditions. The data showed that when asked to move their eyes with the moving ball, as in the Eye Move condition of the localizer task, subjects did so. Subjects maintained good central fixation and did not move their eyes when instructed to fixate centrally and watch the moving ball, using both peripheral and central vision such as required by the Occlude and Disappear conditions.

2.2.2. Localizer task

Activations associated with eye movements were identified by comparing the Fixation condition and the Eye Move condition (Fig. 2). Significant activations were found in two regions: MT/MST and a larger area near the IPS running into the superior parietal lobe. The area thought to be MT/MST overlapped with the region activated to moving ring stimuli. The IPS activation was used to create the IPS ROI used to analyze data in the Main Experimental task.

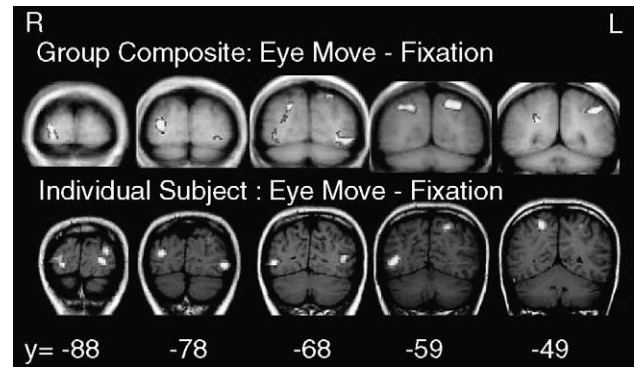


Fig. 2. Composite activation maps at $P < 0.01$ in Talairach space for the localizer task of Experiment 1. ROIs were created from these activation maps. Right is on the left and visa versa. Activations were primarily in MT/MST and superior parietal lobe, extending into the IPS.

2.2.3. Main Experimental task

We compared the Occlude to the Disappear condition, for the Occlude–Disappear event block. We present these data for descriptive purposes. Group contrasts showed activated voxels ($P < 0.01$) in two regions: right MT/MST and bilateral IPS region, with a larger activation in the right IPS (Fig. 3). The IPS activation extended medially into the superior parietal gyrus, or Area 7. An inspection of individual participant data showed some variability in whether the activation was directly on the IPS but all subjects showed activations in the general vicinity of this structure. This activation is slightly more posterior than the IPS activation reported by Cornette et al. (1998b) but is otherwise consistent. Less consistent activations were found in the posterior temporal occipital fossa (PTOF; McCarthy et al., 1995), an anatomical region agreed to be the human analogue of MT/MST.

Individual subject activations were examined using an ROI approach. Two ROIs were defined based on the localizer tasks and percent signal change was calculated for the Occlude and Disappear conditions. The data from each movie was broken into three task components (see Fig. 1). The percent signal change in the ROIs was analyzed using a four-factor ANOVA with ROI region (IPS and MT/MST), condition (Occlude and Disappear), task component (Move 1, Occlude–Disappear event, and Move 2), and hemisphere (left and right), as factors (see Fig. 3 for graphs). Planned comparisons were also conducted. The ANOVA revealed significant differences between ROIs ($F(1, 8) = 5.93$, $P < 0.041$), due to higher signal change in the IPS ROI compared to the MT/MST ROI (mean = 0.29 versus 0.18). The main effect of condition approached significance ($F(1, 8) = 4.49$, $P < 0.067$) due to higher signal change in the Occlude condition. The main effects of task component and hemisphere were not significant, ($F(2, 16) = 1.08$, $P > 0.35$; $F(1, 8) = 2.05$, $P > 0.10$).

There was a significant interaction between ROI and task component ($F(2, 16) = 12.96$, $P < 0.001$), suggesting that the task components had different signal changes in different ROIs. There was a significant interaction between ROI and

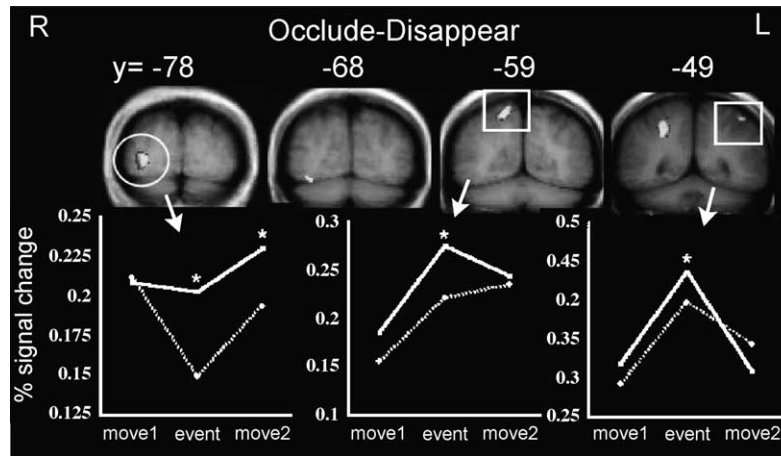


Fig. 3. Composite activation maps at $P < 0.01$ in Talairach space for the Occlude–Disappear comparison in Experiment 1. Right is on the left and visa versa. Talairach coordinates in the y -direction appear above each coronal slice. Below each slice are graphs showing data from the ROI analysis for (from left to right): right MT/MST, right IPS region, left IPS region. Percent signal change is on the y -axis, and task component (e.g. Move 1, Occlude–Disappear event, and Move 2) on the x -axis. The solid line represents the Occlude condition and the dashed line represents the Disappear condition.

hemisphere ($F(1, 8) = 9.71$, $P < 0.014$), suggesting that the ROIs were differentially activated in the two hemispheres. There was also a task component by hemisphere interaction ($F(2, 16) = 9.22$, $P < 0.002$), suggesting that different parts of the motion sequence differentially activated the left or right hemisphere. Lastly, the ROI by condition by task component interaction approached significance ($F(2, 16) = 2.84$, $P < 0.088$), suggesting that the IPS and MT/MST were differentially affected by different parts of the Occlude, as compared to the Disappear, motion sequence. No other interactions were significant.

Planned comparisons were done separately on each ROI. These analyses showed that both right and left IPS were similarly activated to the initial movement (e.g. Move 1) in the Occlude and Disappear conditions ($P > 0.05$; $P > 0.10$). However, when the ball disappeared, there was a higher signal change for the Occlude compared to the Disappear condition, in both the right and left hemispheres ($P < 0.01$; $P < 0.05$). The signal change was similar between conditions for Move 2 in the right hemisphere ($P > 0.5$) but was somewhat higher in the Disappear condition relative to the Occlude condition, in the left hemisphere ($P < 0.06$). These results suggest that *seen* motion similarly affected the IPS but that this area was differentially affected by the occluded motion as compared to the disappearing motion. Namely, activity was higher in the IPS when perceiving occluded motion as compared to motion that suddenly stopped and disappeared.

Planned comparisons in the MT/MST ROI showed that the right and left MT/MST ROIs were similarly activated to Move 1 for both conditions ($P > 0.50$; $P > 0.10$). However, MT/MST had a higher signal change during the Occlude event, as compared to the Disappear event, in both hemispheres ($P < 0.01$; $P < 0.05$). During Move 2, signal remained higher in the right hemisphere for the Occlude condition ($P < 0.05$), but there was no difference between conditions in the left hemisphere ($P > 0.10$). These results are

similar to those found in the IPS: *seen* motion was processed by MT/MST and it continued to process occluded motion, whereas activity dropped during the Disappear event. Activity remained lower in the Disappear condition during Move 2, most likely because conditions had not yet returned to baseline.

For comparison purposes, we created an ROI around an anatomical region that corresponded to primary and second visual cortices in most humans.¹ Percent signal change decreased sharply during the Occlude–Disappear event and then returned to baseline during Move 2. This was reflected in a significant effect of task component, $F(2, 16) = 8.37$, $P < 0.003$. However, there was no difference between the Occlude and Disappear events, $P > 0.20$. There were no other significant effects. This finding suggests that early visual areas primarily process what is actually seen and attended. Because the object of attention, the moving ball, disappeared from view during the Occlude–Disappear event, activity decreased in this ROI but returned to a high level once the object of attention was visible.

2.3. Discussion

The results of Experiment 1 suggest that neurons in the IPS maintain a representation of motion when it briefly disappears, replicating the findings from the pilot study. Less consistent activations were observed in MT/MST. Experiment 1 also found that the regions activated to occluded motion were similar to those subserving pursuit eye movements/and or motion perception. Activations to occluded motion were in the same region but were less extensive and more anterior than those found in the IPS localizer task.

An analysis of a region corresponding to V1/V2 found no difference between conditions and a sharp drop in activity

¹ Imaging time constraints did not allow retinotopic mapping of V1/V2.

during the Occlusion/Disappear event. This finding suggests that early visual areas primarily process what is actually seen and attended. Because the object of attention, the moving ball, disappeared from view during the Occlude–Disappear event, activity decreased in this ROI during both conditions but returned to a high level once the object of attention was visible.

Although the stimuli in the disappear condition had stronger transients than did the stimuli in the Occlude condition, it is very unlikely that transients would lead to the activation patterns reported here. Rather, differences in visual transients, such as flicker, would result in activation patterns that differed in early visual areas such as V1—and our analysis of early visual areas found no differences between conditions.

Experiment 2 was conducted because we could not rule out the possibility that the observed differences in Experiment 1 were due to visually guided actions. Subjects were required to make a keypress at the end of each motion sequence and it is therefore possible that the activations in the IPS reflect the generation of a motor response that differed subtly between conditions. For instance, subjects may have prepared their motor responses earlier in the Occlude condition compared to the Disappear condition because they had more accurate information about the re-occurrence of the target object on the opposite side of the occluder. Non-human primate research suggests that a portion of the IPS region may be involved in visually guided actions (Sakata et al., 1998; Sakata, Taira, Murata, & Mine, 1995).

All stimuli and scanning procedures in Experiment 2 were identical to that used in Experiment 1 except that subjects were not required to make a keypress. The results from this experiment will help to rule out the possibility that subjects used different response strategies in the two conditions.

3. Experiment 2

3.1. Methods

3.1.1. Subjects

Four volunteers participated in Experiment 2. They ranged in age from 18 to 31 years.

3.1.2. Stimuli

As in Experiment 1, there were two types of stimuli used in both experiments: Localizer Stimuli and Main Experimental Stimuli.

3.1.2.1. Main Experimental Stimuli. The Main Experimental Stimuli were identical to those used in Experiment 1.

3.1.2.2. Localizer Stimuli—IPS. Subjects in Experiment 2 were run in a localizer task that was identical to that used for the last three subjects of Experiment 1.

3.1.2.3. Localizer Stimuli—MT/MST. The Localizer Stimuli for MT/MST were identical to those used in Experiment 1.

3.1.3. Task

All aspects of the task were the same as in Experiment 1 except that subjects were not required to make a keypress during the Main Experimental task. The instructions were simply to watch all stimuli passively while maintaining central fixation.

All other aspects of the methods were identical to those used in Experiment 1.

3.2. Results

3.2.1. Localizer task

Activations associated with eye movements were identified by comparing the Fixation condition and the Eye Move condition. Significant activations were found in MT/MST and in the IPS running into the superior parietal lobe. These activations were similar to those found in Experiment 1 (Fig. 2).

3.2.2. Main Experimental task

The only significant activations ($P < 0.01$) to the Occlude–Disappear comparison for the Occlude–Disappear event were found bilaterally in the superior parietal gyrus extending medially into the IPS. Activations were also present in the right MT/MST region at lower thresholds and most likely would have reached significance had statistical power been increased. Fig. 4 shows individual activations for all subjects.

An ROI analysis using the MT/MST and IPS ROIs was conducted as in Experiment 1 (Fig. 4). The percent signal change in the ROIs for the Disappear and Occlude conditions was analyzed using a four-factor ANOVA. There was no significant effect of ROI region ($F < 1$) suggesting that overall activity was similar in the two ROIs. However, there were significant differences between conditions ($F(1, 3) = 10.588$, $P < 0.047$) most likely due to the fact that the Occlude condition had a higher signal change than the Disappear condition, in general (mean = 0.15 versus 0.12; $P < 0.05$). There was a main effect of task component ($F(2, 6) = 5.62$, $P < 0.042$), suggesting that the signal change differed between parts of the motion sequence. There was no main effect of hemisphere, $F < 1$, not significant.

The ROI region factor did not significantly interact with the condition or task component factors. However, there was a significant interaction between ROI region and hemisphere ($F(1, 3) = 21.86$, $P < 0.019$), suggesting that the ROIs were differentially activated in the two hemispheres. The condition by task component by hemisphere interaction approached significance ($F(2, 6) = 3.89$, $P < 0.082$), suggesting that the signal change was differentially affected by different parts of the Occlude, as compared to the Disappear, motion sequence, in different brain hemispheres.

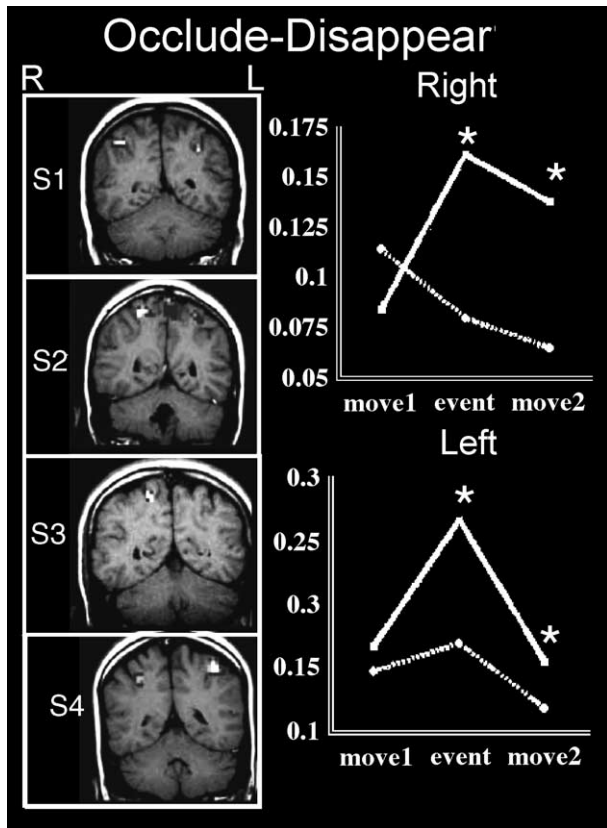


Fig. 4. Individual subject maps for the Occlude–Disappear comparison in Experiment 2 (note that group data was presented for Experiment 1). The graphs reflect the ROI analysis for (from top to bottom): right IPS region, left IPS region. Percent signal change is on the y-axis, and task component (e.g. Move 1, Occlude–Disappear event, and Move 2) on the x-axis. S1 = subject 1, etc. The solid line represents the Occlude condition and the dashed line represents the Disappear condition.

Planned comparisons were done separately on each ROI. These analyses showed that both hemispheres of the IPS were similarly activated in both conditions during the initial motion, Move 1 (R then L; $P > 0.05$; $P > 0.10$). However, when the ball was no longer present on the screen, there was a higher signal change for the Occlude condition in both hemispheres ($P < 0.002$; $P < 0.001$). The signal change remained higher in the Occlude condition during Move 2 ($P < 0.003$; $P < 0.05$) most likely because the signals did not have time to return to baseline.

There were no significant differences between the Occlude and Disappear conditions at the MT/MST ROI except in the right hemisphere, when the ball disappeared in the Occlude condition ($P < 0.05$).

3.3. Discussion

The results of Experiment 2 were similar to that reported for Experiment 1: occluded motion activated the IPS at higher levels than did motion that ceased to exist, as in the disappear condition. This activation overlapped with the IPS

activation in Experiment 1 and there was no significant difference between the IPS activations in Experiments 1 and 2. Activations were also found in the MT/MST region for occluded motion as compared to disappearing motion although this activation did not reach significance. Increasing the power of this study would most likely cause the comparison to reach statistical significance.

These findings provide some evidence that the observed differences in the IPS region found in Experiment 1 reflect a non-motoric representation of the occluded target. Subjects in Experiment 2 did not make a keypress, which tends to rule out the hypothesis that the activations in the IPS were due to visually-guided actions. The evidence from the MT/MST activation is less conclusive because significance levels fell short of 0.05.

4. General discussion

Occluding surfaces in vision are ubiquitous. Shimojo and Nakayama noted that “occlusion is one of the most fundamental facts about vision in daily life” (Shimojo & Nakayama, 1990). The experiments in this paper were designed to answer the question: how does the brain maintain a representation of motion when the moving object moves behind an occluding surface? The main finding of these experiments is that two dorsal stream visual areas were activated when viewing occluded motion. The IPS activation was the most striking and consistent activation, with smaller activations in the human homologue of area MT/MST.

4.1. Attentive tracking and expectations

Attentive tracking of moving targets while maintaining fixation has been previously shown to activate the human IPS region (Culham et al., 1998), a finding that we replicated with a single moving target. However, the IPS is more than a perceptual region. The IPS appears to process motion that is inferred—or expected—but not seen. The first line of evidence comes from cellular recordings in monkeys. Assad and Maunsell (1995) found a population of neurons in the IPS region that responded as though signaling the presence of a moving target, although the moving target was not visible, having moved behind an occluder. In other words, the activity was related to the animal’s presumption that an object was moving through space, even though there was no sensory input indicating that this was happening. The second line of evidence comes from our results. Although little is known about the human homologue of monkey IPS (Rushworth et al., 2001), our results suggest that monkey and human IPS may have similar functions: to maintain a representation of a target both when visible and when not visible. The IPS was activated during seen motion and continued to be activated when a target underwent occlusion. However, if the target simply disappeared instead of undergoing occlusion, activity in the IPS decreased.

It is possible that the IPS is part of the cortical machinery that processes the timing and location of a moving stimulus, seen or unseen, to plan future action. This function would be closely tied to spatial attention, as attention is necessary for tracking moving objects (Yantis, 1992). Spatial attention and eye movements can be dissociated in the laboratory but are closely linked during normal viewing (Colby & Duhamel, 1996). In the case of occlusion, attention is linked to the target even when it becomes invisible whereas it is disengaged when the target disappears. This was surmised by experiments showing that subjects could easily track moving balls when they passed behind an invisible Occluder yet had great difficulties when tracking moving balls that blinked in and out of existence at similar points in space (Scholl & Pylyshyn, 1999).

When objects undergo occlusion, people have various expectations about the fate of the object such as when and where it will reappear. These expectancies—a sort of attention to where and when future events will occur (Olson & Chun, 2001)—is thought to rely on frontal and parietal regions. Kastner, Pinsk, De Weerd, Desimone, and Ungerleider (1999), Kastner and Ungerleider (2000) found that activity in superior parietal regions increased in expectation of an unseen stimulus but that early visual areas did not. These results also point to the conclusion that portions of the superior parietal lobe process aspects of the stimulus that are important for planning future actions, whether the action is a keypress, an eye movement, or just the generation of an expectancy about the fate of an object that is never acted upon.

4.2. Motion perception—both real and implied

A weaker response to occluded motion was found in the human analogue of monkey MT/MST: this area was significantly activated in Experiment 1 and approached significance in Experiment 2. The activation was primarily right lateralized. Although this region has a high density of cells that respond to perceived motion, recent evidence suggests that implied motion activates this area as well. Kourtzi and Kanwisher (2000) showed subjects pictures that contained dynamic information, such as a running man. They compared fMRI activations in this condition to a condition in which subjects viewed pictures that contained no dynamic information, such as a man standing in an upright position. They found that MT/MST and other posterior regions, were activated only when subjects viewed pictures containing dynamic information. A different study using similar stimuli also found that MT/MST was responsive to this type of implied motion (Senior et al., 1999). In addition, area MT/MST has cells that respond both to direction of motion and to the memory of the direction of motion, in the absence of stimulation (Bisley & Pasternak, 2000; Droll, Bisley, & Pasternak, 2000). Although Eskander and Assad (1999) did not find cells in MST that were modulated by occluded motion, it is possible that only a small portion of

cells in this area respond to implied or occluded motion and that these cells were not recorded from. Our results agree with this interpretation inasmuch as the response in MT/MST was weaker than that found in the IPS.

4.3. Eye movements

Areas activated to occluded motion were similar to those activated by smooth pursuit eye movements. The tracking task resulted in activations in the superior parietal lobule that overlapped with those found in the occlusion task but also had a greater posterior extent. There were also activations in the MT/MST region. A great deal of research on non-human primates suggests that portions of the parietal lobe are important in visually guided movements, including smooth-pursuit and saccadic eye movements (Andersen & Gnadt, 1989) and lesions to this area disrupt visually-guided saccades and memory-guided saccades (Pierrot-Desilligny, Rivaud, & Gaymard, 1991). Neural activity related to pursuit eye movements has also been reported in MT/MST (Komatsu & Wurtz, 1988). However, the occluded motion results cannot be explained as being due to smooth-pursuit eye movements or to the generation of a motor response. Subjects practiced attending to the target without eye movements prior to imaging and reported no difficulty in complying with instructions. This was easy to do because the stimuli were large and easy to see. In addition, Experiment 2 had no motor response and there were still activations in IPS and MT/MST.

One possibility that cannot be ruled out is that the conditions differed by the type of intended—but inhibited—eye movements. For instance, during the occluded motion condition, subjects had to refrain from making smooth pursuit eye movements whereas during the disappear condition, subjects had to refrain from making saccadic eye movements to the location that the ball was expected to reappear. Although it is possible that some portion of the observed activations were due to this difference, it seems unlikely that such a subtle difference would lead to the robust IPS and MT/MST activations found in all subjects scanned in Experiments 1 and 2.

4.4. Other brain areas that processes occluded motion

We did not find consistent or noteworthy activations in any other brain regions. To maximize acquisition of images in visual areas of the brain, we did not image anterior portions of the brain. It is possible that other areas participate in this task such as high-level “executive” areas in the frontal lobes, the frontal eye fields, and subcortical ocular-motor regions.

Other types of occluded stimuli may rely on additional processing areas. It is likely that the superior temporal sulcus (STS) helps process occluded biological motion because this area shows high activity levels to various types of biological motion (Puce et al., 1998). Indeed, Baker, Keysers, Jellema, Wicker, and Perrett (2001) recorded from neurons in the monkey STS while the monkey observed the gradual

occlusion of a human. A population of neurons increased activity during the occlusion event and maintained a high level of activity for some time after the experimenter reappeared.

We suggest that the IPS has a general function of maintaining representations of targets for behavior to act upon whereas other regions, such as the STS, have a more specific response profile, such as being activated to a class of stimuli such as moving humans that undergo occlusion. Viewpoint may also dictate which brain areas participate in occlusion tasks. For instance, egocentric occlusion, which occurs when a stationary or moving object becomes occluded because the viewer moved, may depend on different neuron populations than allocentric occlusion, such as studied in this paper. Because occlusion is endemic in the visual world, a variety of neural regions may have solved the problem of how to deal with the problem of how to ready behavior to act upon unseen stimuli.

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