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A Deficit Perceiving Slow Motion After Brain Damage and a Parallel Deficit Induced by Crowding

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Motion perception is known to involve at least 2 kinds of mechanisms—lower level signal detectors and higher level algorithms for comparing object positions over time. When stimulus motion is modal (continuously visible), it is generally assumed that processing via lower level mechanisms is sufficient to make accurate motion judgments. We investigated the possibility that higher level mechanisms may also be involved in the processing of slow motion, even when it is smooth and continuous. This possibility was suggested by results from a brain-damaged patient, JKI, who showed left visual field deficits in both the explicit representation of object position and judgments concerning the direction of slow, but not fast, smooth motion. We investigated the possibility further by using crowding to induce a behaviorally similar motion-perception deficit in healthy observers. Crowding, which is known to impair object-position representation, impaired direction judgments for slow, but not for faster, smooth motion. The results suggest an everyday role for higher level mechanisms in the perception of slow motion, and they reinforce the taxonomy of motion perception in terms of underlying processing mechanisms as opposed to stimulus properties.

Keywords: motion, brain damage, parietal lobe, crowding, object cognition

There are at least two broad ways to engineer a system to detect motion. Suppose a system has been engineered to segment a scene into individuated objects. Suppose that the system also represents the positions of objects, and suppose that it can determine if an object observed at one time is the same (token) as an object observed at another time, even if they are in different positions. Given these capabilities, the system can infer the presence and direction of motion whenever it detects that a specific object occupies a new position.

In contrast, a simpler system can detect and judge motion direction without segmentation abilities and without a need for object representation. Instead, the system can rely on the fact that, under typical circumstances, a moving object will cause transient changes in low-level channels. In particular, a moving object will tend to produce rapid luminance changes as it ceases to reflect light from the positions it leaves and comes to reflect light from the positions it occupies. Without knowing for sure that a moving object causes the change, a system could detect motion fairly reliably through sensitivity to contiguous luminance changes over time.

The distinction between motion perception on the basis of object representation and motion perception on the basis of transients has played a central role in research on motion perception, often referred to as a distinction between higher level and lower level mechanisms (Battelli et al., 2001; Lu & Sperling, 1996, 2001). There are open debates and questions concerning the exact inputs, algorithms, and neural structures that support each system. Broadly, lower level systems are thought to be automatic and preattentive and to take transient signal changes as their only inputs (Adelson & Bergen, 1985; Hock, Gilroy, & Harnett, 2002; Reichardt, 1961; van Santen & Sperling, 1984). Some neurons in the primary visual cortex show these signatures, as do neurons in the middle temporal/medial superior temporal (MT/MST) areas (Britten & Heuer, 1999; Tootell et al., 1995).[1] In contrast, higher level systems are generally thought to rely on focal and object-based attention and to implement algorithms that favor globally minimal mappings when selecting among potential motion trajectories (Burr & Thompson, 2011; Cavanagh, 1992; Dawson, 1991; Petersik, 1995; Ramachandran & Anstis, 1986; Seiffert & Cavanagh, 1999; Ullman, 1984). The brain system supporting these computations probably involves areas that are higher in the hierarchy, including the inferior parietal lobe (Battelli, Pascual-Leone, & Cavanagh, 2007). For purposes of clarity and economy, we refer to the preattentive detection of transient luminance signals as *lower level* and the representation of objects with engagement of selective attention as *higher level*.

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[1] Some studies have shown that attention can also affect the responses of MT/MST neurons (Huk, Ress, & Heeger, 2001). However, these neurons also respond to transient motion stimuli without selective attention. For this reason, MT/MST neurons can be considered part of lower level computational mechanisms despite their midlevel geography.

A second influential distinction in research on motion processing concerns smooth (modal) versus apparent (amodal) motion. We perceive the motion of modal stimuli: objects that remain continually in view. We also complete trajectories despite amodal moments—for instance, when an object becomes occluded (Burke, 1952) or when objects rapidly change position noncontiguously, even across relatively long distances (Braddick, 1974; Petersik, 1989).

It remains unclear exactly how distinctions between smooth and apparent motion map onto higher and lower level systems. It seems likely that higher level systems are necessary in at least some amodal conditions—for example, when noncontiguous position shifts are large and infrequent. But it also appears to be the case that lower level systems detect rapid amodal motion over short distances. Consistent with this view, previous research has shown dissociations between longer range and shorter range apparent motion in the Ternus effect (Petersik, 1989), with longer range motion seeming to rely on higher level mechanisms.

With respect to smooth motion perception, the extent to which both systems may be involved has been less explored. It is known that under conditions that are perhaps unusual in the real world, high-level systems are necessary to perceive some smooth motion. These conditions are usually characterized with regards to the rubric of *second-order* motion, involving equiluminant objects and backgrounds, texture-defined objects, or binocularly defined objects. In these cases, low-level signal modulation is absent by experimental design. Second-order motion demonstrates that higher level systems evaluate the presence of continuous and smooth motion (Seiffert & Cavanagh, 1998, 1999). But it is not clear why. Are high-level systems necessary in more typical circumstances to perceive smooth motion?

It is intuitive to think that smooth motion perception need not usually rely on higher level mechanisms. This appears to be the prevailing, implied view, motivated by the observation that “a rigidly moving object is a drifting modulation of luminance” (Lu & Sperling, 1996, p. 44). Why depend on object representations and algorithms designed to make inferences about unobservable trajectories when one has access to continuously observable low-level signals?

We sought to investigate the possibility that higher level motion systems are required to perceive slow, smooth motion, even that involving local targets with high luminance and background contrast. Smooth motion may typically involve physical luminance changes that could be detected, in principle. But in practice, slow motion may not induce strong enough signals to always produce motion perception.

We were motivated to investigate this possibility by experiments that we conducted with a brain-damaged patient (JKI). The patient presented with impaired visual representation of object position and impaired motion processing for slowly moving, modal stimuli. This could suggest a link between higher level localization representations and the perception of smooth but slow motion—if, that is, the patient’s position-related deficits are what compromised his ability to determine the direction of a smoothly but slowly moving object. In the following, we report the results of our experiments with this patient and those of experiments with healthy participants designed to induce a parallel deficit via crowding, thus testing the possibility that the perception of slow, smooth motion depends on higher level representations of object position.

Experiment 1: JKI’s Spatial-Localization Deficit

Method

Patient history. JKI is a 51-year-old right-handed man with a college education who suffered multiple strokes in 2003. MRI in 2011 revealed bilateral damage (see Figure 1). The damage was more extensive on the right, affecting lateral and inferior surfaces of the temporal lobe, much of the parietal lobe, and the lateral occipital lobe. Damage in the left hemisphere was largely restricted to the posterior parietal lobe and superior occipital lobe. Primary visual cortex was spared in both hemispheres. The right-hemisphere damage included MT/MST areas, which have been associated with motion-signal detection (Tootell et al., 1995).

As a consequence of the right-hemisphere damage, JKI suffers from partial paralysis of the left arm and leg. He also has visual field defects, showing impaired detection of stimuli presented in the lower left visual field and in the medial portion of the lower right visual field. JKI also reports frequent diplopia (double vision) with binocular but not monocular viewing.

Neuropsychological testing revealed intact language and memory but significant visuospatial deficits characteristic of patients with bilateral parietal damage (e.g., Di Pellegrino & De Renzi, 1995; Humphreys & Riddoch, 1993; Robertson, Treisman, Friedman-Hill, & Grabowecky, 1997). In particular, JKI is severely impaired in copying simple pictures or designs, producing fragmented and inaccurate copies; he is impaired in reaching for visual targets in the upper left visual field, despite being able to detect the targets; and he shows extinction/simultanagnosia for upper left visual field targets, often failing to report a target if another target is presented further to the right. Some of these deficits are described in greater detail later.

Apparatus and test setting. All testing with JKI took place in a dim room. Stimuli were generated with MATLAB Version 2014a (MathWorks, Natick, MA) and the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) and were presented on a MacBook Pro (Apple Inc., Cupertino, CA) laptop with a refresh rate of 60 Hz. The viewing distance was fixed to 55 cm so that the whole display subtended 29.6° × 18.5° of visual angle. A chin rest helped JKI maintain a stable posture and fixation. The protocols of this and all the reported experiments were approved by the Homewood Institutional Review Board of Johns Hopkins University.

Fixation during testing was monitored informally and corroborated by a small number of eye-tracker sessions. Eye-tracker calibration and testing were strenuous for JKI, which limited our ability to collect sufficient data. But performance appeared qualitatively similar with fixation maintained during those sessions.

Because of JKI’s lower visual field defects, all stimuli in the experiments reported here were presented in the upper half of the visual field. Also, to prevent double vision during testing, JKI’s right eye was patched throughout all of the experiments.

Procedure. We investigated JKI’s ability to detect and localize objects in the upper visual fields. Each trial involved presentation of either one or two objects for 750 ms. JKI was asked to report the color and shape of each object seen during a trial.

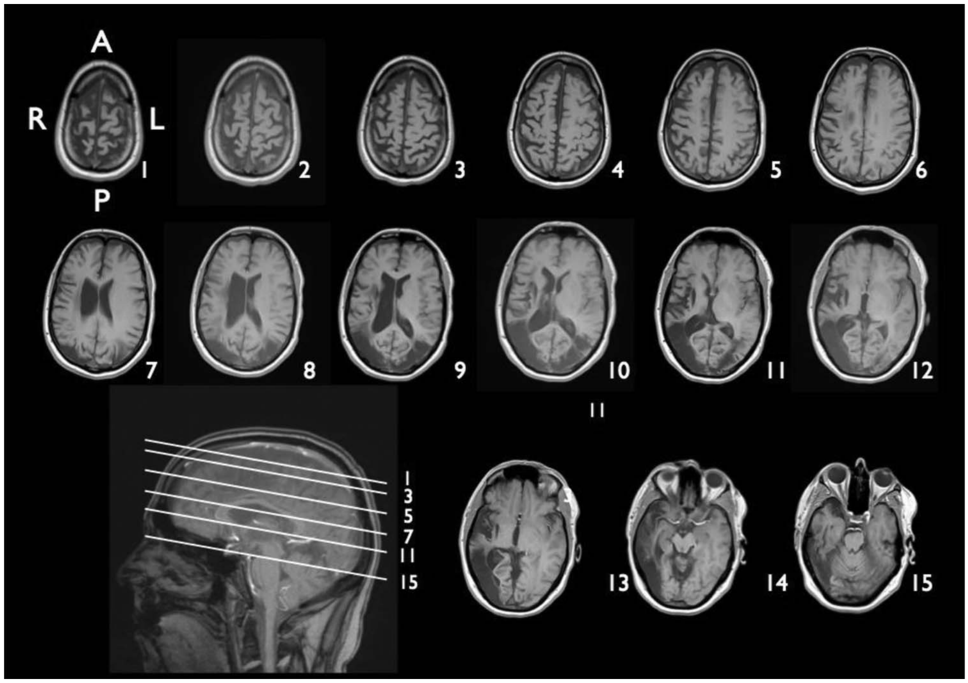

Figure 1. T1-weighted magnetic resonance images of patient JKI's lesion, presented in a series of axial images (1–15) and an inset showing the location of the slices on a sagittal image. A = anterior; R = right; L = left; P = posterior.

In addition, JKI was asked to report the location of each object. The objects were constrained to a black strip 6° above fixation. The strip (28° × 2.31°) was further divided into 10 equally spaced horizontal positions (2.8° apart from one another, measured center to center; see Figure 2). Objects always appeared in one of these 10 locations, and on two-object trials, the objects always appeared in two different positions (and with different shapes and colors). JKI was familiarized with the numbering of these 10 locations from −5 to +5, as shown in Figure 2, and his understanding of this numbering system was confirmed via testing with free viewing (i.e., without fixation) and with a tactile apparatus. Position numbers were not displayed during the experiments.

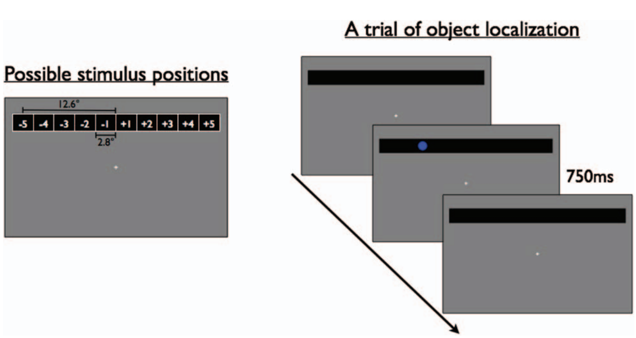

Figure 2. Procedure used for investigating patient JKI's object-representation deficits in Experiment 1. Each trial included one or two colored shapes that appeared in 10 possible positions. JKI's task was to report the shape, color, and location of any stimulus objects he observed on a trial. See the online article for the color version of this figure.

Results

The likelihood that JKI correctly reported the color and shape of an object as a function of its position on the screen in the single-object trials is graphed in Figure 3. JKI was able to accurately report the shape and color of an object presented in the upper right visual field. In the upper left visual field, his performance was also relatively good (mean accuracy = 95%), though he occasionally missed some objects presented at positions −5 and −3. These results suggested that JKI has little or no deficit in detecting a single, briefly presented object in either of the upper visual fields.

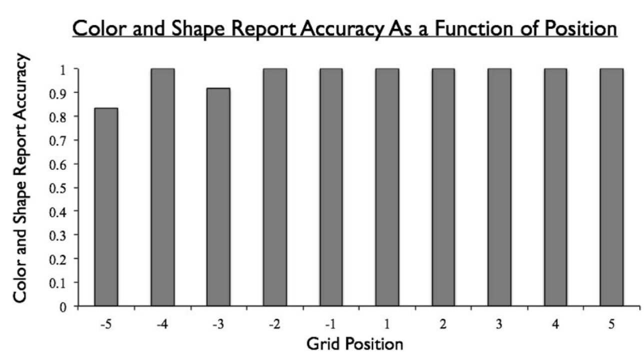

Figure 3. Patient JKI's color- and shape-reporting accuracy as a function of object position in single-object trials in Experiment 1. Objects were randomly presented in one of 10 positions. Accurate responses involved reporting both the shape and the color of the object that appeared. Results are plotted as a function of an object's actual position, but this does not imply that JKI reported the relevant object as being in that position.

(With two objects presented simultaneously, performance in the left visual field showed evidence of extinction or simultanagnosia. In particular, JKI frequently failed to report the leftmost stimulus when that stimulus appeared in the left visual field. The implications of the two-object results are outside the scope of this report).

We also analyzed JKI's position reports in single-object trials. The average locations at which JKI reported an object as a function of objects' actual locations are shown in Figure 4. He demonstrated an inability to accurately report object locations in the left visual field, even when he could accurately report the colors and shapes of the relevant objects. His deficit was systematic, with objects generally reported farther toward the vertical meridian (i.e., to the right) than they actually appeared. In the upper right visual field, in contrast, his position reports were generally accurate.

Discussion

Although misreaching for visual objects is common among optic ataxia patients (Rossetti, Pisella, & Vighetto, 2003), localization deficits at the perceptual level are less frequently reported. We are aware of two other patients who showed similar localization deficits. Di Pellegrino and De Renzi (1995) reported a patient, DG, who suffered primarily right temporal lobe damage. Similar to JKI, DG often transposed a stimulus that was presented in the left visual field to the right of its true location. Another patient, RM, who has bilateral parietal damage, also showed impairment in visual-localization tasks (Baylis & Baylis, 2001; Friedman-Hill, Robertson, & Treisman, 1995; Robertson et al., 1997). However, because of the nature of the tested tasks, it is not clear whether RM also systematically localized objects to the right of their true locations. It is worth investigating single-object localization with other patients in a more systematic way, because it is possible that such deficits fail to become noticed when accompanied by additional impairments.

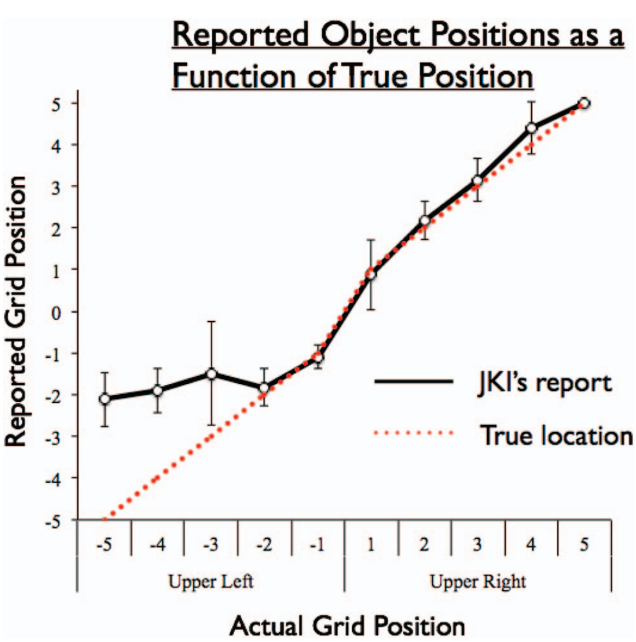

Figure 4. Patient JKI's average reported grid positions in single-object trials as a function of objects' true positions in Experiment 1. Error bars show standard deviations (nine trials per position). See the online article for the color version of this figure.

For current purposes, the main implications of these initial evaluations are that JKI appears to have a deficit of object-position representation in the upper left visual field. In the upper right visual field, however, he appears largely unimpaired. This led us to investigate JKI's motion-perception abilities, reasoning that in the upper left visual field, he should show impairment in any motion-perception task that relies on an intact system for representing object position. In contrast, he might possess preserved abilities with motion perception that arises more directly from lower level signals.

Experiment 2: JKI's Smooth Motion Perception

Method

To test JKI's ability to perceive the direction of continuously moving stimuli, we conducted an experiment in which, on each trial, a white disk moved a fixed distance of 1.39°. The disk's speed varied by trial; we used six different speeds (1.95°/s, 0.97°/s, 0.49°/s, 0.32°/s, 0.24 °/s and 0.19°/s) to cover a wide range, including two relatively fast speeds (around 1°/s or greater) and four relatively slow speeds (less than 0.5°/s).

The disk subtended 0.9° in diameter and had a luminance of 198 lx. It could move either to the left or right. We used three anchor positions (4.16°, 5.54°, and 6.93° away from central fixation cross, around the ±2, ±3, and ±4 grid positions in the localization experiment) as the starting and ending positions of motion in each visual field. On each trial, motion was restricted entirely to either the left or the right visual field; stimulus objects never crossed the vertical meridian. For each trial, two adjacent positions (e.g., 4.16° and 5.54° to the left of fixation) were selected as the starting and ending locations. Throughout the disk's horizontal motion, its vertical position was fixed at 6° above fixation. The background was black, producing strong contrast with the disk.

Each trial was initiated by an experimenter after JKI indicated that he was fixated and ready. JKI's task was to report verbally whether the disk had moved to the left or to the right. Testing was divided into several blocks across several weeks. In total, JKI completed 24 trials with each speed in each visual field.

Results

JKI's directional judgment accuracy is shown in Figure 5. In the right visual field, his performance was nearly perfect (98.6%), and there was no significant effect of motion speed, $\chi^2(5, N = 144) = 7.15$, $p = .21$, Cramér's $V = .22$. In the left visual field, he showed a speed-dependent impairment, with worse performance under the slow speed conditions. A chi-square analysis showed a significant main effect of speed, $\chi^2(5, N = 144) = 18.16$, $p = .003$, Cramér's $V = .36$. We then averaged JKI's performance with the two faster speeds and compared that with his average performance with the four slower speeds. There was a significant difference between the two fast and four slow speeds, $\chi^2(1, N = 144) = 16.90$, $p < .001$, Cramér's $V = .34$.

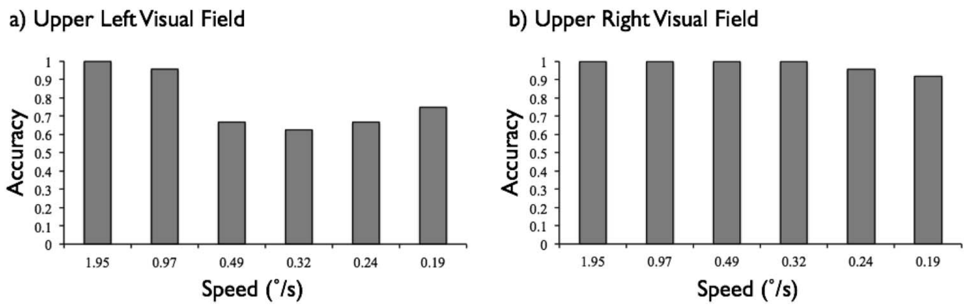

Figure 5. Patient JKI's directional judgment accuracies as a function of speed in the upper left and upper right visual fields in Experiment 2.

Discussion

In the left visual field, JKI's ability to judge the motion direction of a slowly but continuously moving local target was considerably impaired compared with his ability with faster moving targets and with targets at any of the tested speeds in the right visual field. Note that because we fixed motion distance across all speed conditions, slower motion produced targets displayed for longer durations. Hence, JKI's impaired perception of slow motion occurred despite the longer durations over which to assess motion direction.

The motion-perception results, in conjunction with JKI's deficit in position representation, are consistent with the hypotheses that JKI generally uses higher level position-comparison mechanisms to evaluate slow motion. For slow motion, the luminance change in the spatial–temporal domain is much less rapid than that for fast motion, and, thus, transient signals alone are not strong enough to reliably support low-level motion perception.

Of course, we cannot entirely exclude the possibility that JKI simply has unrelated position and motion deficits. Especially given the presence of damage in the right middle MT/MST areas, it is possible that JKI suffers from a motion signal–detection impairment that differentially interacts with motion speed. We are unaware, though, of any reports of hemifield-restricted low-level motion deficits induced by MT/MST brain damage; recall that JKI's performance in the right visual field appeared spared and did not interact with motion speed. Moreover, the intriguing possibility suggested to us by JKI's pattern of deficits is that higher level mechanisms may usually play a compensatory role in slow, smooth motion perception whenever low-level signals are impotent, whether because of extenuating factors such as brain damage or because they are simply too weak.

We therefore sought to further explore the hypothesis that perception of slow, continuous motion relies on higher level mechanisms and that JKI's associated deficits reveal a dependency that applies in neurologically intact observers as well. Normal observers may not distinguish intuitively between faster and slower smooth motion because both are usually detectable. Below the surface, however, faster and slower motion may rely differently on lower and higher level mechanisms. Faster motion may rely on luminance changes (and may also benefit from redundancy with higher level mechanisms), whereas slower motion perception may rely more heavily on higher level mechanisms, owing to gradually attenuated low-level transient signals as speed decreases. In Experiment 3, we investigated this hypothesis.

Experiment 3: A Motion-Perception Deficit Induced in Healthy Participants via Crowding

JKI's deficits suggested to us the possibility that in general—that is, in healthy, visually normal observers—the perception of slow, continuous motion relies heavily on higher level systems, perhaps because any transient luminance changes are separated by durations much larger than the typical settings of low-level detectors. A way to test this possibility is to impair high-level abilities in healthy observers and then determine whether a slow, smooth motion impairment emerges as a consequence.

Toward this end, we used spatial crowding. For objects presented in the visual periphery, nearby flanker objects impair an observer's ability to discriminate and localize individual objects, a phenomenon known as *crowding* (Intriligator & Cavanagh, 2001; Pelli & Tillman, 2008; Whitney & Levi, 2011). The exact nature and causes of crowding-induced impairments remain debated (e.g., Levi, Hariharan, & Klein, 2002; Pelli, Palomares, & Majaj, 2004; Wilkinson, Wilson, & Ellemberg, 1997). Some theorists have suggested, for example, that crowding impairs the ability to allocate object-based attention to individual objects, in turn impairing any mechanisms that rely on object-based attention, including individuation (e.g., He, Cavanagh, & Intriligator, 1996; Intriligator & Cavanagh, 2001). For current purposes, the important consequence of crowding is an impaired ability to localize individual objects accurately. Whether this is a primary impairment that results in further consequences—such as an inability to allocate attention, or vice versa—is beyond the scope of the current research.

Via crowding, we sought to devise a motion-judgment experiment as similar as possible to the one used with JKI. A white circle was shown to participants in the periphery, at one of four possible speeds, and under conditions with and without crowding inducers. The task was to report the direction of the moving target. We reasoned that if crowding makes it difficult to extract high-level information about object position and slow motion produces low-level signals that are too weak, then crowding should impair motion-direction judgments for slow stimuli (compared with uncrowded stimuli, from which high-level information can be extracted).

Experiment 3a: Primary Experiment

Method: Participants. Twenty-two undergraduate students at Johns Hopkins University participated in this experiment for course credit. All had normal or corrected-to-normal visual acuity.

Method: Stimuli and procedure. Stimuli were presented on a Macintosh iMac computer (Apple Inc., Cupertino, CA) with a refresh rate of 60 Hz. The viewing distance was approximately 60 cm so that the whole display subtended 39.4° × 24.8° of visual angle.

The moving stimulus was a white disk that always moved a distance of 0.64° on a trial at a speed of 1.53°/s, 0.64°/s, 0.14°/s, or 0.08°/s. It was always presented in the peripheral field of one of the four possible quadrants (i.e., upper left, upper right, lower left, or lower right), starting its motion 9° (diagonally) from the central fixation cross (see Figure 6). A demonstration of these conditions and all those reported can be viewed online at http://www.jhuvisualthinkinglab.com/maetal-motiondeficit.

In the crowding condition, four static flanker disks (identical with the moving one) were presented surrounding the moving target disk, as shown in Figure 6, at positions 2.39° to the right and left of the moving disk's starting position and also 1° directly above and below. In the no-crowding condition, the moving disk was presented alone in one of the four possible quadrants. The four static flanker disks were presented in one of the other three quadrants.

Participants were instructed to fixate a central cross. Fixation was not monitored, but a secondary task was used to encourage fixation. At a random point during each trial, a single digit (between 1 and 9) replaced the fixation cross for 167 ms. At the end of each trial, participants first pressed the left or right arrow key on the computer keyboard to indicate the motion direction they observed on that trial, and then they entered the digit that had appeared at fixation. Each participant completed 48 trials for each combination of crowding condition and speed—a total of 384 trials per participant.

Results. We excluded from analysis all trials with an inaccurate digit report, which amounted to 8.7% of trials. Motion-judgment accuracies are presented in Figure 7. There was a significant main effect of speed, $F(3, 63) = 13.61$, $p < .001$, $\eta_p^2 = .39$, and a significant main effect of crowding, $F(1, 21) = 14.47$, $p = .001$, $\eta_p^2 = .41$. Critically, there was a significant Speed × Crowding interaction, $F(3, 63) = 6.70$, $p < .001$, $\eta_p^2 = .24$.

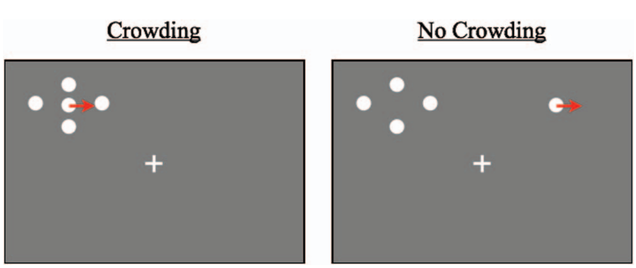

Figure 6. Schematic depiction of stimuli under conditions of crowding and no crowding in Experiment 3a. The moving disk could appear in any of the four quadrants (upper left, upper right, lower left, or lower right). On each trial in the crowding condition, flanker objects were present in the same quadrant as (and surrounding) the moving object; on each trial in the no-crowding condition, they were present in one of the remaining three quadrants. All of the flanker objects remained static during a trial. See the online article for the color version of this figure.

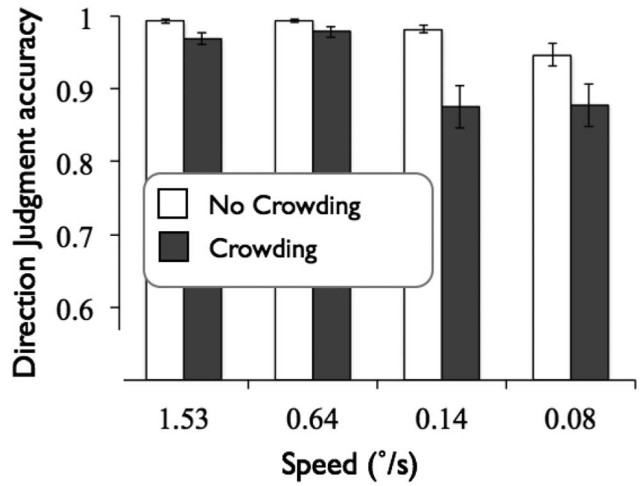

Figure 7. Directional motion-judgment accuracies as a function of object speed and crowding condition in healthy participants in Experiment 3a. Error bars represent standard error of the mean.

To further scrutinize the effect of crowding, we looked at the simple main effect of crowding as a function of speed. Crowding had a significant effect on performance at the two slower speeds (with Scheffé correction): 0.08°/s, $F(1, 21) = 11.8$, $p = .002$, and 0.14°/s, $F(1, 21) = 28.5$, $p < .001$. However, it did not significantly affect performance at the faster speeds (with Scheffé correction): 0.64°/s, $F(1, 21) = 0.57$, $p = .46$, and 1.53°/s, $F(1, 21) = 1.38$, $p = .25$. Participants performed significantly worse with crowded stimuli, but only at slower speeds.

Discussion. Judging the motion direction of a slowly moving peripheral target proved more difficult for healthy, visually normal observers when flankers crowded the slow-moving target. Crowding is known to impair higher level object individuation and localization abilities. Accordingly, these results are consistent with the hypothesis that the perception of slow, smooth motion requires higher level object-based mechanisms, whereas faster motion can rely entirely on low-level signal transients that are available despite crowding.

Experiment 3b: Low-Level Signal Control

A critical piece of the aforementioned hypothesis is that the slow motion used in this experiment (and in the experiments with JKI) produces low-level signals that are too weak to effectively support motion perception and direction judgments, even when uncrowded. We conducted an additional experiment designed to verify that the slow speeds used here are too weak, when uncrowded, to induce strong motion perception.

An additional goal of the experiment was to determine whether crowding in these displays greatly dampens low-level motion signals. Does crowding reduce the quality of low-level signals rather than preclude reliance on high-level mechanisms? This distinction is of concern because lower level motion detection requires the integration of signals within a local region (Britten & Heuer, 1999; Burr & Thompson, 2011), and receptive field sizes in the middle temporal visual area (MT) are relatively large and dependent on eccentricity (Felleman & Kaas, 1984). We have acknowledged the possibility that JKI's impairment with slow motion reflects low-level impairment, possibly caused by MT damage, and differentially affects slow motion because it is simply more difficult to process than is fast motion. Here, the issue was a symmetrical one with respect to crowding: Might crowding generally dampen low-level processing, ultimately showing a larger effect with slower moving stimuli?

This control experiment used a motion-adaptation aftereffect. This is a classic illusion in which one fixates while viewing an adaptation stimulus moving in one direction and subsequently perceives a static stimulus as moving in the opposite direction (Anstis, Verstraten, & Mather, 1998).

Adaptation is generally thought to be a low-level phenomenon. Its neural basis resides in MT/MST areas, and it can happen even under conditions of divided or redirected visual attention (Huk et al., 2001). With a relatively fast speed (a Gabor moving at six cycles/s and spatial frequency of 0.52 cycles/°), Whitney (2005) showed that a motion aftereffect could be produced despite spatial crowding.

We applied a similar logic in our control experiment. If our slow motion stimuli inherently produce weak signals, then they should fail to produce motion aftereffects when uncrowded, and the degree of any adaptation should be independent of crowding. To show that crowding does not dampen low-level signals—parallel to the logic of Whitney's (2005) experiment—the fast speeds should produce adaptation even when crowded, and, again, crowding should not influence the degree of adaptation.

Method: Participants. Twenty-three graduate and undergraduate students at Johns Hopkins University participated in this experiment for course credit. All had normal or corrected-to-normal visual acuity. Ten participants completed the slow speed condition, and 13 participants completed the fast speed condition. The results from three participants in the fast speed condition were excluded from analysis because debriefing revealed that they mistook the instructions as guiding them to report the motion direction of the adaptation stimulus. Ten participants successfully completed the experiment in each of the speed conditions.

Method: Stimuli and procedure. Stimuli were similar to those used in the main experiment, except as discussed later. For the adaptation stimuli, we only used two of the speeds from Experiment 3a: 1.53°/s (fast) and 0.14°/s (slow).

Motion duration is known to be a factor that interacts with crowding. With the slow speed (0.14°/s), the exact conditions used in the previous experiment would result in motion duration sufficient for adaptation (Rajimehr, Vaziri-Pashkam, Afraz, & Esteky, 2004). But for the fast condition (1.53°/s), if the target disk were to move the same distance as in the slow condition, the total duration would only amount to 0.5 s, too short to induce a motion aftereffect.

We therefore made the following modifications. In the fast motion condition, the total motion distance was doubled to 1.28°, and motion repeated for five consecutive cycles. For example, for leftward motion, when the object reached the leftmost position, it returned (unseen) to the starting position and then moved along the motion path again. To prevent rapid transients when the object returned to its starting position, we placed an invisible occluder at the start and endpoints of the motion path so that the object began its motion by seamlessly disoccluding and ended by seamlessly becoming occluded. A schematic depiction of the stimuli is shown in Figure 8 (and a dynamic demonstration is available online).

Participants were asked to fixate throughout, and the same digit task as in Experiment 3a was used to encourage cooperation. Participants were instructed to focus on the digit task during each trial. After peripheral motion was completed, the moving disk and crowding inducers were replaced by a static red disk (the test stimulus) that appeared in the moving disk's final position. In addition, two black vertical lines were presented together, above and below the red disk, and aligned with its center (see Figure 8).

The task was to press one of two buttons to report whether the red disk was shifted leftward or rightward relative to the black lines. Participants were told that if they perceived the red disk as moving, they could also make the button press based on its motion direction. Digit reports were made subsequent to directional reports at the end of each trial. As in Experiment 3a, half of all trials were uncrowded, with crowding inducers located in one of the three quadrants that did not contain the motion stimulus in the respective trial.

We used a between-participants design with respect to speed to prevent participants from attempting to diagnose the relevance of speed in the experiment. Crowding was a within-participant factor, however.

Results. Accuracy of digit report was again very high: 95% on average. And again, we excluded from analysis all trials with inaccurate digit responses.

An adaptation effect would appear as a tendency to report alignment of the static test stimulus in the opposite direction from the motion direction during the adaptation phase. We thus coded trials as either consistent or inconsistent with a motion-adaptation effect. Then we calculated the proportions of trials with the aftereffect. Results are shown in Figure 9.

To analyze the adaptation results, we performed a 2 × 2 split-plot ANOVA with speed as a between-participants factor and crowding as a within-participant factor. There was a significant main effect of speed, $F(1, 18) = 11.87$, $p = .003$, $\eta_p^2 = .40$. However, there was no significant main effect of crowding, $F(1, 18) = 3.13$, $p = .094$, $\eta_p^2 = .15$. The Crowding × Speed interaction was also not significant, $F(1, 18) = 0.22$, $p = .232$, $\eta_p^2 = .016$.

We also conducted four independent post hoc one-sample *t* tests to compare the average adaptation score in each condition with the expected baseline of .50 (i.e., equally mixed responses, unrelated to the motion direction of the inducing stimulus). When the motion speed was fast (1.53°/s), significant adaptation effects were present in both the crowding, $t(9) = 2.99$, $p = .015$, Cohen's $d = 0.94$, and no-crowding conditions, $t(9) = 3.00$, $p = .015$, Cohen's $d = 0.95$. With the slow speed (0.14°/s), however, neither the crowding, $t(9) = 1.69$, $p = .13$, Cohen's $d = 0.53$, nor the no-crowding condition, $t(9) = 0.29$, $p = .78$, Cohen's $d = 0.09$, induced a significant motion aftereffect.

Discussion. This experiment supplied the two kinds of evidence sought. The slow motion stimuli, even when uncrowded, failed to induce a reliable motion aftereffect. This suggests that those stimuli produce relatively weak low-level motion signals.

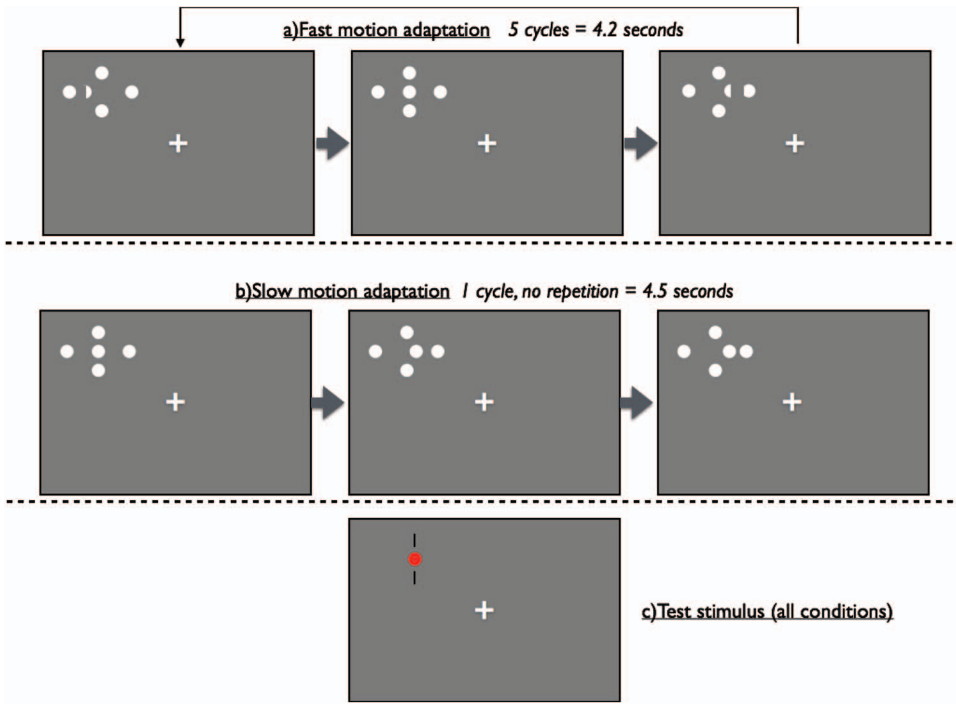

Figure 8. Schematic depiction of stimuli in the motion-adaptation experiment (3b). (a) With fast motion, repeated cycles were necessary to extend the total duration of motion observed. To facilitate this, an object disoccluded to begin motion and then became occluded as a cycle ended, with each trial consisting of five repeated cycles in approximately 4.2 s. (b) For slow motion, one cycle was completed on each trial, taking approximately 4.5 s. Rightward and crowded motion examples shown in Panels a and b. (c) Uncrowded motion was included in the experiment as well. The test stimulus was always a static red disk between two guidelines. Participants reported whether they perceived the disk as displaced rightward or leftward relative to the guidelines. See the online article for the color version of this figure.

This is consistent with the hypothesis that perception of the motion direction of such stimuli depends on higher level mechanisms.

Second, there was no effect of crowding on the strength of (significant) adaptation induced by the faster moving stimuli. This suggests that crowding, at least as constructed in these displays, does not lead to the disruption of low-level signal integration, consistent with previous work on crowding and adaptation (Rajimehr et al., 2004; Whitney, 2005).

General Discussion

We first presented a brief case study of a patient, JKI, who suffered widespread brain damage, including extensive bilateral parietal lesions. JKI was found to have two associated deficits largely restricted to the left visual field. First, he could not accurately localize the position of an object, although he could almost always report the object's shape and color. Second, he was impaired in judging the direction of slowly but continuously (modally) moving targets without impairment for faster moving targets (or for any motion in the right visual field). Broadly, JKI's motion-perception deficit minimally demonstrates that lower level motion detectors are tuned to faster speeds.

We are unaware of any reports of similar slow motion difficulty either in a patient study or via experimental manipulation. There is, however, the well-known case study of LM, a patient with motion blindness—that is, the inability to perceive motion (Zihl, von Cramon, & Mai, 1983; Zihl, von Cramon, Mai, & Schmid, 1991). In contrast to JKI, under many circumstances, LM is unable to detect or perceive motion as it unfolds (and the speeds tested in the relevant studies tended to be faster than any of the speeds we investigated here). But she can make directional judgments relatively accurately. She appears to achieve this through input from higher level mechanisms, comparing an object's current and remembered positions. In her words, "First the target is completely at rest. Then it suddenly jumps upwards and downwards" (referring to vertical motion; Zihl et al., 1991, p. 2244). Thus, LM appears not to possess the phenomenological experience of stimulus motion, although she does appear to possess the higher level, position- and object-based mechanisms that seem unavailable to JKI's left visual field.

It could be that the difference between LM and JKI is a dissociation not between phenomenal experience and higher level judgment mechanisms but between phenomenal experience and lower level signal integration. JKI's neurological condition may simply have made him more susceptible than normal to the inherent difficulty of perceiving slow motion with low-level detectors, with the implication that his motion deficit is unrelated to his spatial-representation deficit. This concern

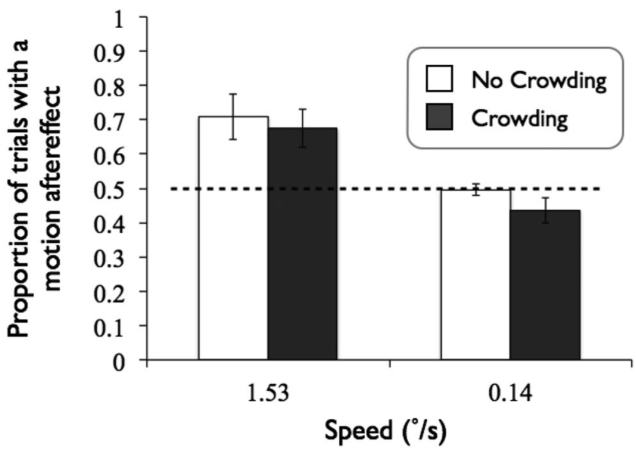

Figure 9. Proportions of trials showing a motion aftereffect as a function of object speed and crowding condition in Experiment 3b. A motion aftereffect (adaptation effect) involves a directional report opposite the motion direction of the inducing stimulus. Thus, the figure shows proportions of trials on which an opposite direction report was given. An absence of adaptation should produce equally mixed reports. Error bars represent standard error of the mean.

was especially salient given some damage in JKI's MT/MST areas.

Although we determined that distinguishing between these possibilities would be difficult in the case of JKI, we sought to investigate the association between position representation and slow motion perception in healthy observers. Specifically, we investigated the possibility that normal perception of slow, smooth motion might rely heavily on higher level mechanisms that depend on representation of a target's position. To our knowledge, this is a novel hypothesis, investigation of which bears on broader theories about the organization of motion perception in the human mind and brain.

To test our hypothesis, we induced a slow motion–perception deficit in visually normal observers via crowding. The crowding inducers in these experiments were static. Their purpose was to make it difficult for an observer to resolve the current position of a moving target within the flanked region, as crowding is known to impair the resolution of object individuation spatially and to limit an observer's ability to allocate object-based attention (Intriligator & Cavanagh, 2001; Pelli & Tillman, 2008; Whitney & Levi, 2011). Of course, we cannot say that crowding induces representational or attentional deficits like those of JKI. But it is worth noting that previous studies of parietal lobe damage have frequently reported deficits of object-based attention and individuation (e.g., Baynes, Holtzman, & Volpe, 1986; Robertson et al., 1997). It would be interesting for future work to investigate directly whether crowding produces deficits that are similar to deficits that often follow parietal lobe damage, such as simultanagnosia, extinction, and neglect.

The slow motion deficit experienced by healthy observers under conditions of crowding further suggested that low-level mechanisms might not generally participate in the representation of slow, modal motion. To investigate this possibility further, we used an adaptation paradigm and found that, whether crowded or not, our slow motion stimuli did not produce motion aftereffects. The critical result here is that even the uncrowded slow-moving stimuli failed to produce effects, though they should have if they sufficiently stimulated low-level motion detectors. Moreover, in the same experiment, fast-moving stimuli did induce aftereffects, both when crowded and when uncrowded. Crucially, crowding did not significantly influence the strength of this effect. These results suggest that crowding impairs perception of slow motion not because it exacerbates the challenges of detecting motion on the basis of weak signals—because no evidence of exacerbating effects was obtained—but, instead, because crowding precludes a reliance on compensatory high-level motion detection when slow motion produces weak signals.

These results are also consistent with influential theories suggesting that higher level mechanisms of motion perception depend on object-based attention (Burr & Thompson, 2011; Cavanagh, 1992; Petersik, 1995; Seiffert & Cavanagh, 1999), and they are generally consistent with theories that draw a taxonomy of motion stimuli in terms of the underlying algorithms that can process those stimuli rather than in terms of inherent stimulus features, such as being modal (smooth) versus amodal (apparent; e.g., Seiffert & Cavanagh, 1998, 1999).

In general, one may wonder why the visual system has evolved to use two distinct motion systems. Providing a comprehensive answer to this question is beyond the scope of our data. But our results do suggest that the systems are to some degree complementary rather than redundant. The lower level system efficiently detects quick luminance transients, but such a system will always depend on the sensitivity setting of its constituent detectors. It appears that those detectors may have been set with temporal and spatial parameters that produce false negatives with respect to continuous but slow motion (perhaps in an effort to otherwise reduce false positives). Fortunately, higher level mechanisms can compensate by relying on representation of token position and perhaps by exploiting object-based attention to improve spatial resolution.

This perspective is consistent with additional ways in which the two systems may be complementary, even compensatory. The smooth motion system suffers from the aperture problem (Adelson & Movshon, 1982), whereas feature tracking needs to solve motion correspondence between features (Ullman, 1979). It may also be that lower level mechanisms are best for detecting motion direction, with coarse-grained direction sensitivity (Hildreth, 1984), whereas higher level mechanisms can disambiguate motion direction when necessary (Shimojo, Silverman, & Nakayama, 1989). And more recently, it has been suggested that binocular feature tracking is necessary to overcome the inverse problem of local binocular three-dimensional motion perception (Lages, 2013; Lages & Heron, 2010; Pierce, Bian, Braunstein, & Andersen, 2013).

Conclusion: An Everyday Role for High-Level Motion Perception

We presented two main results. First, we reported that a patient with an object-localization deficit restricted to one visual field also showed a deficit for the perception of slow, modal motion in that visual field. Second, we reported that crowding impairs the ability to perceive slow, modal motion. The first result, though circumstantial, is consistent with the hypothesis that slow, modal motion perception generally relies on representation of object position as opposed to low-level signal detection. The second result constitutes strong evidence in favor of that hypothesis.

High-level motion mechanisms are often invoked to explain what can seem like motion illusions, the perception of motion under contrived viewing conditions and in places where it is not clear that one should see motion—for instance, in cases of long-range apparent motion or texturally defined second-order motion. For higher level mechanisms to explain illusions under atypical, fabricated conditions, they should be useful and relatively accurate under typical circumstances. Whole-object occlusion is one frequent occurrence for which high-level mechanisms are likely necessary. The results that we have reported suggest that slow and steady motion is one as well.

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