

# Visual motion detection sensitivity is enhanced by orthogonal induced motion

**Hiromasa Takemura**

Department of Life Sciences, The University of Tokyo,  
Tokyo, Japan



**Ikuya Murakami**

Department of Life Sciences, The University of Tokyo,  
Tokyo, Japan



Visual motion information passes through several distinct stages including local motion processing in an earlier stage, followed by global motion processing at a later stage. However, the stage at which the perceptual limit of detection arises remains unknown. In order to examine which stage is critical for motion detection, we investigated how vertical illusory motion affected detection performance for physical horizontal motion. We introduced illusory induced motion, such that a central pattern would be perceived as moving in the opposite direction to the surrounding motion, even though the central stimulus was physically stationary. We presented the central Gabor patch, which was barely moving to the left or right, together with a surrounding grating moving vertically. Subjects were asked to judge whether the central stimulus was moving left or right, and thus the illusory vertical motion itself was task-irrelevant. We found that the performance on the horizontal test was enhanced when it was combined with the induced vertical motion, which resulted in the central motion appearing slightly oblique rather than purely horizontal. Our results indicate that the later stage, in which motion integration and center-surround interaction appears, is critical for determining the perceptual limit of motion detection.

Keywords: visual motion, induced motion, motion integration, illusion

Citation: Takemura, H., & Murakami, I. (2010). Visual motion detection sensitivity is enhanced by orthogonal induced motion. *Journal of Vision*, 10(2):9, 1–13, <http://journalofvision.org/10/2/9/>, doi:10.1167/10.2.9.

## Introduction

### Perceptual limits of motion detection and hierarchical visual motion processing

Although much sensory information is transmitted to the cortical visual system, most of it does not appear in our visual perception, possibly because tiny fragments of local information disrupt visual constancy. For example, our retinal image is constantly moving due to fixational eye movements. However, such motion information does not arise in ordinary visual perception, and we normally see the stationary world as stationary even when such local information is represented at an earlier stage of cortical visual processing (Murakami, 2003; Murakami & Cavanagh, 1998, 2001; Sasaki, Murakami, Cavanagh, & Tootell, 2002). According to the recent review by Ross and Burr (2008), the visual system regards weaker signals as “default conditions” to prevent the impact of noisy local input and internal noises on visual images. In the case of visual motion processing, the default condition is stationary, and the visual system should discard weaker local motion signals at some stage of processing. In the psychophysical literature, such a perceptual limit of motion detection is presumably reflected in the minimum-motion threshold. The purpose of the present study involved

investigating the functional stage of visual motion processing at which the perceptual limit of visual motion detection (minimum-motion threshold) is determined. This motion detection performance is defined in terms of the rate of correct responses to questions involving a two-alternative directional judgment about a barely moving stimulus between two opposing directions, i.e., left vs. right. Thus, the term “detection” in the present study refers to providing the correct response for a task requiring directional discrimination between two motion directions.

It is well known that visual motion processing has several distinct stages. Earlier-stage processing is carried out by directionally selective neurons with spatially confined receptive fields, which are thus thought to process local spatiotemporal correlations of light stimulation through biological filters tuned to particular spatial and temporal frequencies in limited receptive fields. Later-stage processing is believed to be carried out within larger neuronal receptive fields using more complex and global motion information based on spatial integration and spatial differentiation of adjacent motion signals with center-surround antagonistic receptive fields and directional combinations of separate local component motions into one global pattern motion. This idea of hierarchical processing is supported by previous studies from psychophysical, physiological, and computational disciplines

(Adelson & Movshon, 1982; Castelo-Branco et al., 2002; Huk & Heeger, 2002; Movshon & Newsome, 1996; Rodman & Albright, 1989; Simoncelli & Heeger, 1998; Wilson, Ferrera, & Yo, 1992). However, the stage at which the perceptual limit of motion detection performance arises remains unknown. The purpose of the present study was to investigate which stage of processing determines the perceptual limit of visual motion detection.

One line of evidence indicates that motion perception depends on the information processed at the earlier stage (for simplicity's sake, we hereafter refer to relatively early subsections and relatively later subsections of the motion processing hierarchy as the “earlier stage” and the “later stage,” respectively). Welch (1989) reported that the speed-discrimination threshold for a moving plaid (i.e., the linear sum of two drifting gratings of different orientations) reflected the speed of component gratings rather than the speed of the plaid itself. Other psychophysical investigations have also supported the idea that global motion is computed from internally processed local component motions rather than physical ones (Derrington & Suero, 1991; Stone, Watson, & Mulligan, 1990). These findings suggest that the earlier stage dealing with local motion processing determines the perceptual limit of motion detection.

However, the information contained at the earlier, local motion processing stage is still ambiguous from the viewpoint of the “aperture problem” (Hildreth, 1984). At this stage, local motion information is processed within spatially limited receptive fields, and the true velocity of the stimulus cannot be determined because an infinite number of solutions is possible along a constraint line. According to the hierarchical processing schema, the visual system solves the problem through motion integration mechanisms at the later stage (Adelson & Movshon, 1982). In this context, information at the earlier processing stage does not represent perceived motion. Indeed, many neurophysiological and neuroimaging studies have supported the idea that the activity of the cortical sites belong to the later stage; for example, area MT correlates highly with visual motion perception (Britten, Newsome, Shadlen, Celebrini, & Movshon, 1996; Ditterich, Mazurek, & Shadlen, 2003; Newsome, Britten, & Movshon, 1989; Salzman, Murasugi, Britten, & Newsome, 1992; Serences & Boynton, 2007). However, establishing which cortical sites correlate with motion perception does not solve the question of what stage of processing limits motion detection performance because global motion processing strongly depends on local motion processing, as described above.

Two hypotheses about hierarchical visual motion processing and the perceptual limit of motion detection can be proposed.

**First Hypothesis:** The local motion processing stage determines the perceptual limit of motion detection. Information about the local motion components with

subthreshold speeds is not transmitted to the later global motion stage and cannot be integrated with other motion signals.

**Second Hypothesis:** The global motion processing or later stage determines the perceptual limit of motion detection. Information about some local motion components with subthreshold speeds is transmitted to the global motion processing stage and can be integrated with other motion signals.

To determine which hypothesis is correct, we must examine whether local motion components with subthreshold speeds can be integrated with other motion components. In the present study, we examined the interaction between the horizontal motion component, which is very slow and cannot be detected if it is presented independently, and the additive vertical motion component.

## Relationship between motion direction and motion detection sensitivity

Before conducting the main experiment, we performed a preliminary experiment to examine how motion detection performance might be modulated by the motion direction. In this first experiment, a random-dot pattern in a blurred window moved in one of two possible directions that were mirror-symmetrical about the vertical midline. The observers (the two authors) were asked to evaluate whether the horizontal motion was directed to the left or to the right (Figure 1A).

The performance in response to the slightly oblique direction (22 deg vs. 158 deg) seemed to be slightly better than that in response to the purely horizontal direction (0 deg vs. 180 deg), but the difference was not significant (Figure 1C). Thus, detection is not strongly enhanced by a small change in the motion direction (e.g., 22 deg) if the speed of motion remains unchanged. Figure 1D shows the results of a different analysis. As depicted in Figure 1B, we decomposed the physical speed of the oblique motion into the speeds of the vertical and horizontal motions. In Figure 1D, we replotted the results of Figure 1C according to the speed of the horizontal motion. In this case, the performance in response to movement in the oblique direction (22 deg vs. 158 deg) was significantly better than that in response to movement in the horizontal direction. Thus, at an identical horizontal velocity, the performance is better in response to oblique than to horizontal motion. However, this performance modulation by motion direction can be easily explained. Indeed, the dots used in this comparison always moved faster by  $1/\cos(22^\circ)$  in the oblique than in the horizontal direction even though their horizontal components had an identical velocity (as described in Figure 1B). Therefore, this preliminary experiment using locally oblique motions cannot clarify whether the local or global stage is more critical.

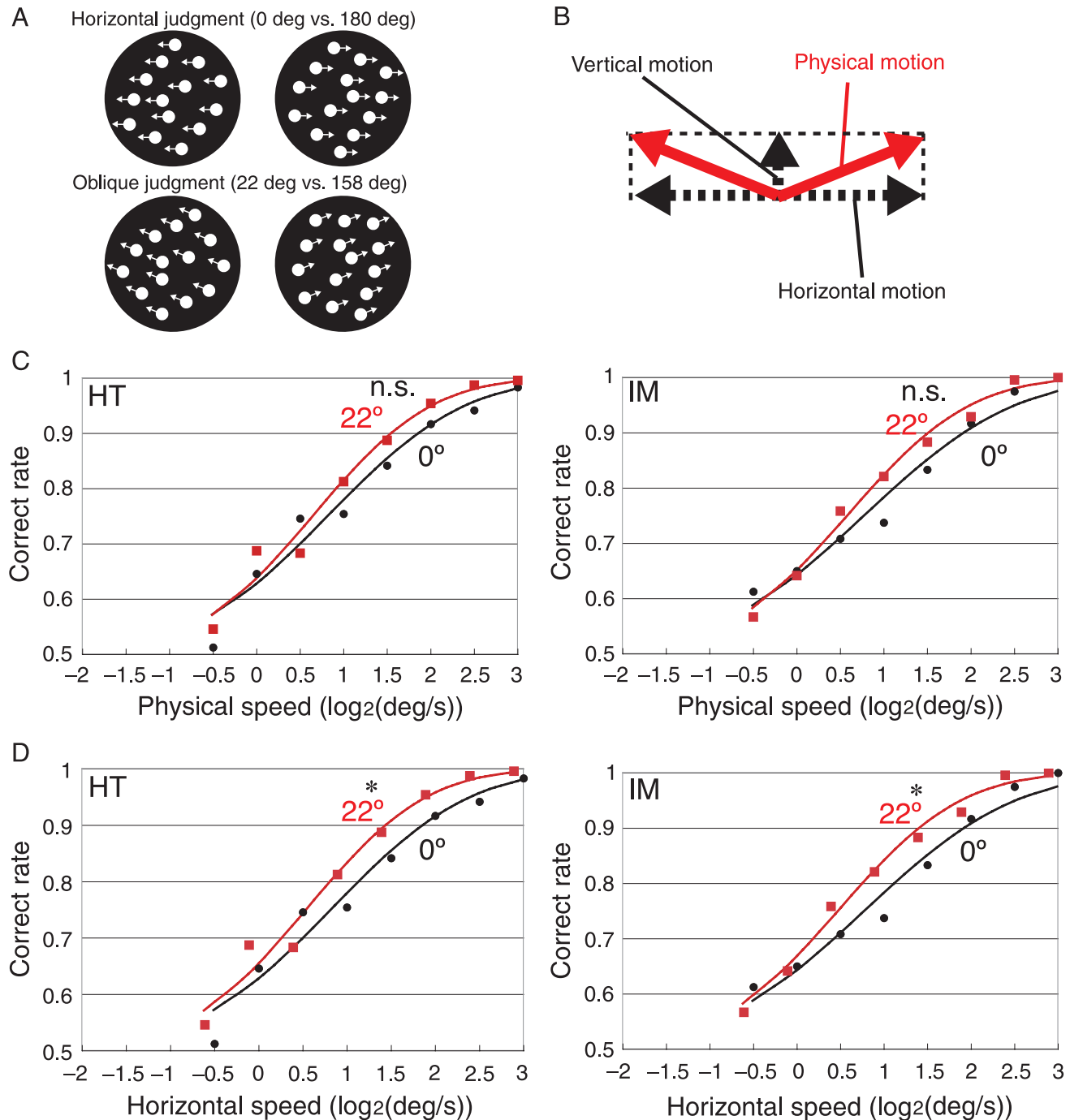


Figure 1. Preliminary experiment. (A) Schematic figure of the experimental task. (B) Schematic illustration of the physical and horizontal speeds of motion. The red arrow represents the physical motion of stimuli, and black dotted arrows represent decomposed “horizontal” and “vertical” motions. (C–D) Results of the preliminary experiment. Each chart shows the results for each observer (HT and IM). The vertical axis of each chart indicates the correct response rate, and the horizontal axis indicates the (C) physical motion speed or (D) horizontal motion speed. The “0” on the abscissa corresponds to 0.01465 deg/s. The correct response rate of each data point was based on 240 trials of directional judgment. Different colors indicate different direction conditions (black: 0 deg vs. 180 deg, red: 22 deg vs. 158 deg). Curves are the best-fit cumulative Gaussian functions for each direction condition. The asterisk indicates the significant levels of the differences between the minimum-motion thresholds under the two direction conditions based on 1999 Monte Carlo simulations of the distributions of threshold and slope differences; \* indicates  $p < .05$ .

Instead, in the present study, we set the locally horizontal motion at around the detection threshold, and added a vertical motion so that the perceived direction should be oblique as a result of motion integration process. If the earlier stage were critical for determining the perceptual limit of motion detection (the first hypothesis discussed above), the detection performance for horizontal motion would not be influenced by the existence of vertical motion because the subthreshold horizontal motion component would not be transmitted to a later stage. On the other hand, if the later stage were critical (the second hypothesis), the subthreshold horizontal motion could be integrated with the vertical motion, and the motion representation would become oblique at a later stage. In this case, the detection performance would improve in comparison with that for the purely horizontal motion without any vertical motion because, at an identical horizontal velocity, detection of oblique motion is easier than detection of horizontal motion, as indicated in [Figure 1D](#).

### Previous studies on motion integration and motion detection sensitivity

Many previous studies have examined the relationship between motion integration and motion detection performance by investigating the integration of two motion components using a plaid (Adelson & Movshon, 1982). Derrington and Badcock (1992) found motion detection performance improved when motion was integrated with an orthogonal component by using the plaid. This result supports the second hypothesis, that a subthreshold motion component can be integrated with an orthogonal component and produces global motion with a faster speed. However, Derrington and Badcock interpreted their enhancement effect in a different context. They inferred that the visual system is equipped with a mechanism for “feature tracking” that helps to improve performance by detecting a second-order contrast-defined feature (“blob”) necessarily contained in the plaid. From this perspective, the results of the previous study were not sufficient to address our research question because the effect could also be explained by feature tracking.

To clarify this point, the present study investigated how the detection of horizontal motion was affected by vertical motion that was not present in the stimulus but created at the later stage of motion processing (i.e., illusory motion). Illusory motion does not influence any physical feature of the target stimulus, and we were able to exclude the influence of any visual feature of the stimulus, such as those detected by feature tracking in the case of the plaid, by using this type of motion.

In the present study, we used a well-known illusory motion called “induced motion,” in which a physically stationary stimulus appears to move in the direction

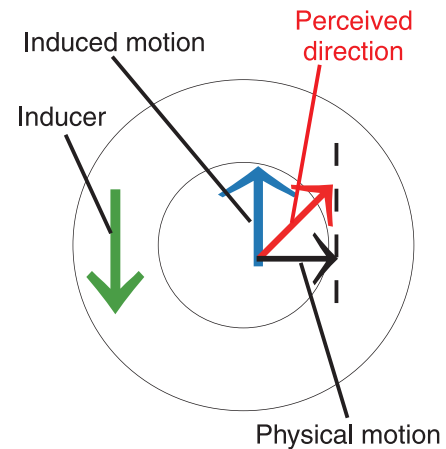


Figure 2. Schematic representation of the integration of horizontal physical motion and vertical illusory motion.

opposite to that of the surrounding motion (Duncker, 1929; see Reinhardt-Rutland, 1988 for review). One of the important characteristics of the induced motion is that it changes depending on eccentricity, stimulus size, and luminance contrast (Murakami & Shimojo, 1993, 1996; Tadin, Lappin, Gilroy, & Blake, 2003). These characteristics of induced motion correspond with the feature of “center–surround antagonism” in the receptive fields of area MT and MSTl neurons, in which the response to the preferred direction within the classical receptive field is suppressed when the same direction of motion is simultaneously presented in a surrounding area outside the classical receptive field (Allman, Miezin, & McGuinness, 1985; Eifuku & Wurtz, 1998; Perge, Borghuis, Bours, Lankheet, & van Wezel, 2002). These studies suggest that the perception of induced motion might partly reflect center–surround interactions that are more frequently encountered in neurons at higher cortical sites. Whatever the neural correlate might be, we will give a functional definition to the later stage as the stage at which neural computation for induced motion and its directional interaction with physical motion takes place.

In our experiment, a central stimulus was surrounded by a clearly moving stimulus (called the “inducer”), and the central stimulus was not stationary but barely moved horizontally at a speed near the motion detection threshold. The surrounding stimulus moved in a vertical direction, so an illusion of vertical motion was induced in the central stimulus. As a result, the central stimulus appeared to move in an oblique direction ([Figure 2](#)). By testing how the orthogonal induced motion affected the perceived direction of the central stimulus (Experiment 1) and how it affected detection performance for the horizontal motion component (Experiment 2), we examined the relationship between hierarchical visual motion processing and motion detection sensitivity.



## General methods

### General methods

#### Subjects

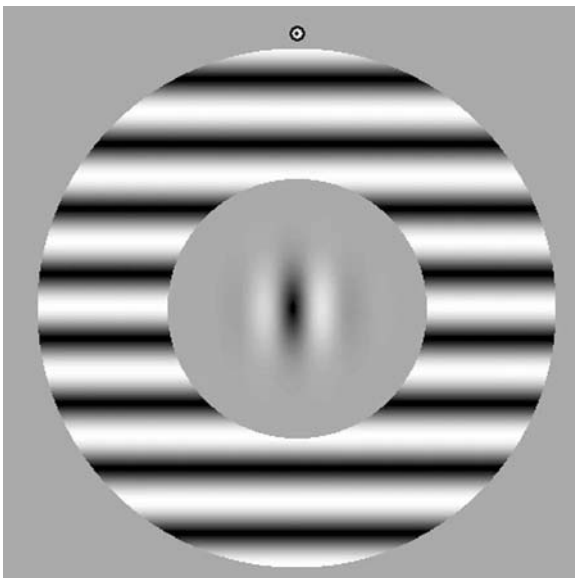
This study followed the Declaration of Helsinki guidelines and was approved by the Ethics Committee of the College of Arts and Sciences, the University of Tokyo. Five subjects (aged 20–39, three of whom were naïve to the purpose of the experiments) with normal or corrected-to-normal vision participated. Each subject gave written informed consent and passed a battery of tests on visual acuity, astigmatism, and stereopsis.

#### Apparatus

The stimuli were generated by computer (Apple Power-Mac G5) using Psychtoolbox (Brainard, 1997; Pelli, 1997) and were displayed on a 22-inch CRT monitor (Mitsubishi Electric RDF223H, 1152 × 870 pixels, refresh rate 75 Hz, 0.038 deg/pixel, driven by a videoboard with 10-bit depth.) The viewing distance was 50 cm. The mean luminance was 38.4 cd/m<sup>2</sup>. Subjects viewed all stimuli binocularly in a dark room.

#### Stimuli

The stimulus display was composed of a central stimulus and a surround stimulus, as shown in [Movie 1](#).



Movie 1. Demo movie of the stimulus. The surrounding stimulus moves downward and the central stimulus moves rightward. The surround speed is 2.34 Hz, and the central speed is 0.4 Hz, which, for illustrative purposes, is faster than the one we used in the actual experiment.

The central stimulus was a Gabor patch ( $SD = 2.58$  deg), whose carrier drifted leftward or rightward within the stationary contrast envelope. The surround stimulus was a sinusoidal grating drifting upward or downward within an annular window (inner and outer diameters 7.5 deg and 15 deg, respectively). The background was uniform gray. For both stimuli, the spatial frequency was 0.53 cycles/deg, and the luminance contrast was 0.99. The speeds of the stimuli differed across conditions and are expressed as values of temporal frequency in hertz throughout the text. The fixation point was provided at 8 deg above the center of the central stimulus.

#### Procedure

Each trial began with the presentation of the fixation point; after 200–500 ms, the inducer was presented. After 500–700 ms, the Gabor patch was presented for 500 ms with the inducer. Immediately after the presentation, stimuli were masked by random dot noise for 500 ms to exclude any influence of motion aftereffects. The stimulus duration was confirmed as sufficiently long for the occurrence of motion integration in a pilot experiment. After the masking, subjects were requested to press one of two computer keys in response to the motion seen (see Methods in each experiment). The fixation point remained until the end of masking.

### Experiment 1: Motion direction matching

Subjects were asked to match the perceived motion direction of the Gabor patch with an arrow-shaped visual icon by rotating the icon with a mouse cursor, or to press a canceling button when they perceived the Gabor patch as being stationary. No feedback was given.

The speed of the inducer was 0 (stationary), 0.04, 0.3, or 2.34 Hz, and the speed of the Gabor patch was 0 (stationary), 0.0125, 0.025, or 0.05 Hz. The speed and motion direction (left or right) of the Gabor patch and the motion direction (up or down) of the inducer were randomized within each session. From session to session, the speed of the inducer was changed in random order. Each session consisted of 80 trials. Each subject completed six sessions under each inducer-speed condition. Subjects received at least one practice session under each condition prior to actual data acquisition.

### Experiment 2: Motion detection sensitivity

The surround inducer was stationary (0 Hz), moving vertically at 0.01, 0.02, 0.04, 0.07, 0.15, 0.3, 0.59, 1.17, or 2.34 Hz, or was a counter-phase flicker at 0.04, 0.3, or 2.34 Hz.

Subjects were asked to report the horizontal motion direction of the Gabor patch from a fixed choice of two alternatives, left or right. An auditory feedback signal was delivered after each response. The central patch was often perceived to move obliquely depending on inducer speed, but subjects were asked to judge only the horizontal motion direction that physically applied to the central patch, irrespective of how large the illusory motion they might be experiencing was. Note that the surrounding motion component and illusory induced motion component were irrelevant to the task; the vertical component was of no help in horizontal motion detection from a geometrical point of view.

The central Gabor patch was equivalent across inducer speeds. Its speed (0.0125 or 0.025 Hz) and motion direction (left or right) were randomized within each session. The motion direction of the inducer (up or down) alternated between successive trials to prevent accumulation of motion adaptation. From session to session, the inducer speed was changed in random order. Each session consisted of 76 trials. Each subject completed 18 sessions with each inducer speed and at each temporal frequency of the counter-phase flicker, and 36 sessions with the stationary inducer. For one naïve subject, inducer speed was limited to from 0.01 to 0.3 Hz. Prior to data acquisition, subjects had at least one practice session under each condition.

## Results

### Experiment 1: Motion direction matching

Prior to the main experiment (Experiment 2), we examined how induced motion influenced the perceived direction of the central Gabor patch that was drifting leftward or rightward.

In 3.1% of all trials, subjects pressed the cancellation button because the Gabor patch did not appear to move. The percentage of canceled trials under each condition is shown in Figure 3E, and we summarized the data for the remaining 96.9% of the trials.

Figures 3A–3D show how the perceived motion direction of the central stimulus changed toward the vertical direction of the induced motion. When the inducer was stationary, the patch was seen to move horizontally in most cases (Figure 3A). This horizontal preference was observed even when the central speed was 0.0125 Hz, which was below the conventional detection threshold. Thus, by default, the clearly visible vertical orientation of the carrier grating apparently biased the directional matching toward horizontal. However, when the inducer moved, the patch appeared to move obliquely, revealing a bias toward the direction of induced motion (Figure 3C). This effect became more robust when the inducer moved

faster; in some cases, the central patch appeared to move almost vertically (Figure 3D; e.g., when the center moved at 0.0125 Hz and the surround moved at 2.34 Hz). These results clearly show that the perceived direction of the central patch changed depending on the speeds of the inducer and the central patch.

In Figure 3F, the median perceived direction is plotted against the surround speed, with the central speed as the parameter. Under the simplistic assumptions that all the tested speeds were faithfully registered in the visual system and that the perceived direction equaled the weighted average of the (default) horizontal direction and the vector sum of the horizontal speed of the central patch and the vertical speed of the induced motion, the perceived direction of the central stimulus was formulated as

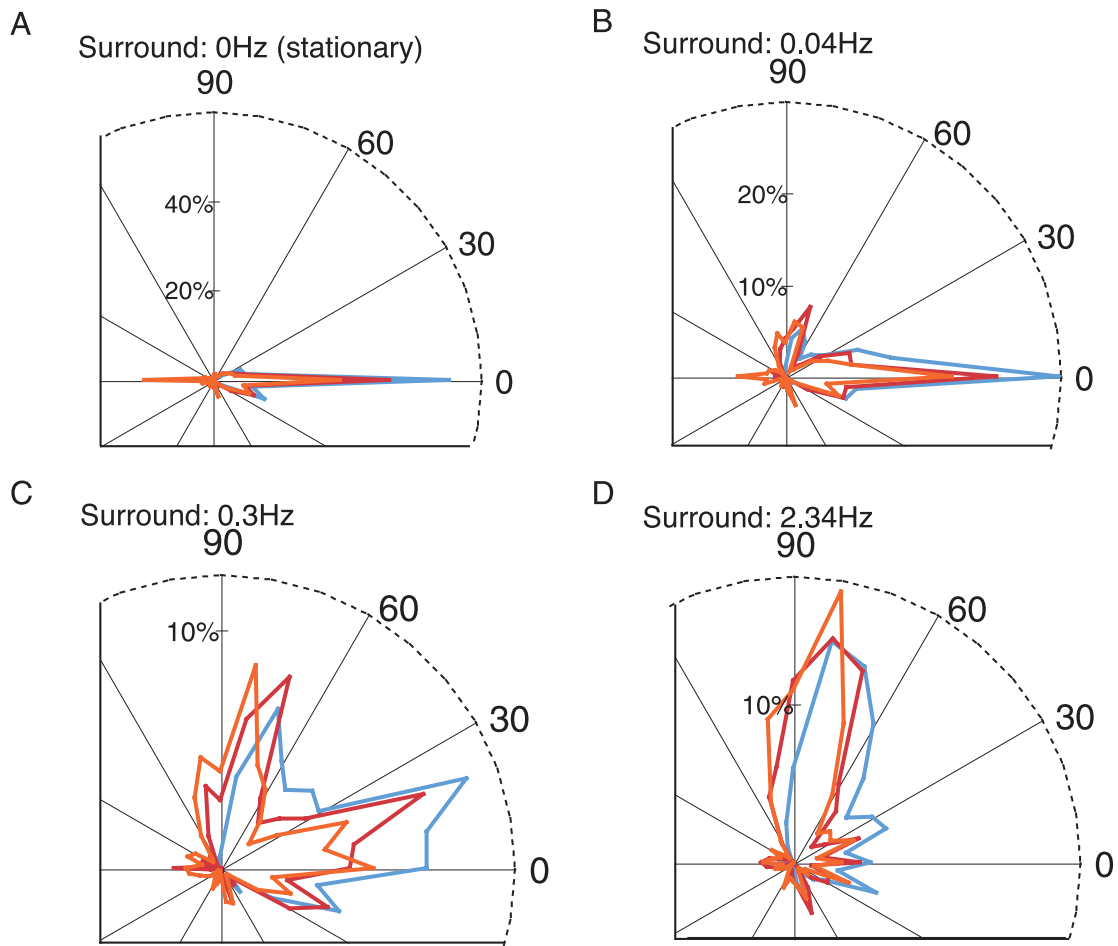
$$y = a \arctan(gs/c), \quad (1)$$

where  $s$  and  $c$  indicate the speeds of the central and surrounding stimuli, respectively,  $a$  indicates the relative weights of the averages of the default and biased responses,  $g$  indicates the ratio of induced-motion speed to inducer speed, and  $y$  denotes perceived direction (rightward is 0, counterclockwise is positive). This simplistic model yielded a surprisingly good fit to the actual data ( $a = 0.88$ ,  $g = 0.046$ ,  $R^2 = 0.99$ ), as shown in Figure 3F.

### Experiment 2: Motion detection sensitivity

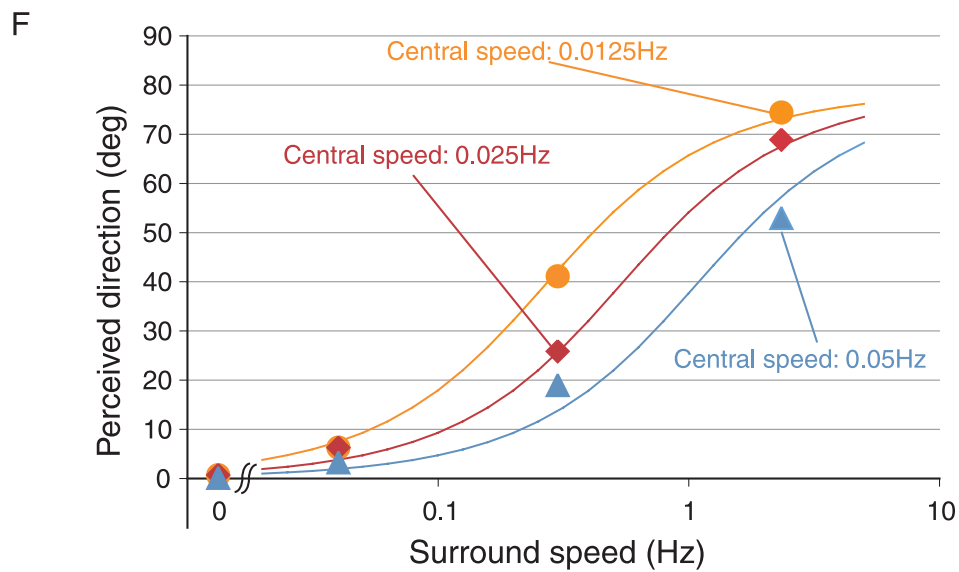
In Experiment 2, we defined motion detection sensitivity as the rate of correct responses to tasks involving two-alternative directional judgments about horizontal motion (leftward or rightward) at very slow speeds (0.0125 and 0.025 Hz, or 1.42 and 2.83 min/s). These speeds fell within the range of the lower threshold of referenced motion found by previous measures (Murakami, 2004; Shioiri, Ito, Sakurai, & Yaguchi, 2002), and thus, the correct response rate could be expected to be above chance but well below 1.

Figure 4 shows the correct response rate of directional judgment against inducer speed. The data for the easier (0.025 Hz) and harder (0.0125 Hz) central speeds are overlaid. When the inducer moved at <0.04 Hz, the performance was indistinguishable from that obtained with the stationary surround. When the inducer moved at >1 Hz, motion detection sensitivity was either degraded (two-tailed  $z$ -test,  $p < 0.005$ ) or unaffected, depending on central speed. Surprisingly, however, we obtained a contrasting effect when the inducer speeds were within an intermediate range (0.04–0.3 Hz): in both central speeds, motion detection performance was significantly enhanced (two-tailed  $z$ -test,  $p < 0.001$ –0.05) in comparison with the performance obtained with the stationary



**E**

Cancel button rate	Surround			
	0Hz	0.04Hz	0.3Hz	2.34Hz
Center 0.0125Hz — orange	11%	9.2%	2%	1.5%
Center 0.025Hz — red	8.8%	6.5%	0.8%	0.8%
Center 0.05Hz — blue	1.5%	0.8%	0.6%	0.8%



surround. In terms of the detectability index ( $d'$ ) of signal detection theory, the sensitivity was enhanced by 0.15 at 0.0125 Hz and by 0.25 at 0.025 Hz.

The degradation of sensitivity with faster inducer speeds could be understood in many ways in the framework of signal-to-noise ratio. First, the high temporal frequencies contained in the surround inducer might mask the near-threshold motion in the center as we shall argue shortly in this section. Second, the presence of the task-irrelevant motion at high speeds might work as a distracter capturing attention and other processing resources. Third, as a result of motion integration between physical motion and induced motion, the Gabor patch is perceived to move almost vertically, as was shown in Experiment 1. This strong bias toward vertical might make horizontal directional judgment difficult.

On the other hand, the enhancement of sensitivity in intermediate inducer speeds is surprising. The stationary-surround condition in this experiment consisted of a motion stimulus surrounded by a stationary frame of reference. This stimulus configuration has long been used to assess the lower limit of the detection of referenced motion (Legge & Campbell, 1981; Murakami, 2004; Shioiri et al., 2002; Tyler & Torres, 1972) to which the human visual system is most sensitive. Also, the spatial parameters of the stimulus configuration were chosen to be optimal at the tested eccentricity (McKee & Nakayama, 1984; Murakami, 2004; Murakami & Shimojo, 1996). The excellent baseline performance obtained under this condition is consistent with previous measurements (Murakami, 2004; Shioiri et al., 2002). Hence, the current knowledge within the vision sciences does not predict that

Figure 3. Results of Experiment 1. (A)–(D) Histograms indicate the response rates (i.e., the number of completed trials over all trials) for the perceived direction of the central patch in each surround speed; “0” indicates purely rightward, and “90” indicates purely upward. This format was used to indicate the perceived direction of the central patch when it was physically moving rightward and the surrounding stimulus was physically moving downward (and thus the induced motion in the central patch was expected to occur in the upward direction). Data obtained under mirror-symmetrical conditions were reversed and merged. Data for all subjects were merged. The across-subjects histogram for the surround speed of 0.3 Hz (panel C) might appear bimodal, but this shape is attributable to individual variability in response peaks; the distributions for some subjects peaked at approximately 20 deg, whereas those for others peaked at approximately 75 deg. In any case, the histogram for each individual was not significantly bimodal (Hartigan’s Dip Test;  $p > 0.2$ ). (E) The percentage of trials in which subjects did not report the perceived direction but pressed the cancellation button because they perceived the central patch as stationary. (F) Median of perceived direction plotted against inducer speed. Each colored line is the best-fit curve for each central speed based on the simplistic model described in the main text.

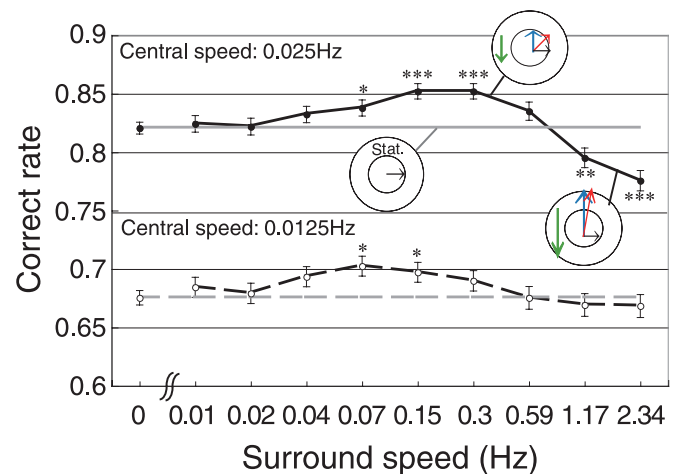


Figure 4. Results of Experiment 2. The correct response rate is plotted against inducer speed. The curves indicate the correct response rates obtained with the moving surround, and the shaded lines indicate the baseline performance, namely the correct response rates obtained with the stationary surround. Error bars indicate  $\pm 1$  SEM. Asterisks indicate the significance levels of the differences from the baseline performance; the symbols \*, \*\*, and \*\*\* indicate  $p < .05$ ,  $p < .01$ , and  $p < .001$ , respectively.

detection performance will improve over that obtained at baseline.

Note that the stimulus configuration, including local motion information of the Gabor patch and instructions given to the subjects, was equivalent across conditions. If local motion processing at the early stage of visual motion processing were the only important factor in determining motion detection performance, the performance would not be influenced by induced motion. However, in our results, the correct response rate increased along with the influence of induced motion. For this increase to be possible, the cortical site that is responsible for minimum motion detection must have access to neural signals mediating the perception of induced motion and its directional integration with physical motion. This suggests that the later stage, in which multiple motion components are integrated, plays an important role.

However, as we varied the speed of the inducer, we actually varied its temporal frequency. In a concentric stimulus configuration, the temporal frequency of the surround could affect the perceived contrast of the central stimulus (Takeuchi & De Valois, 2000). To dissociate the effect of the motion (inducing vertical illusory motion in the central stimulus) and the temporal frequency of the surround, we conducted an experiment under a control condition using a counter-phase flickering stimulus with the same temporal frequency as the moving inducer. This stimulus thus contained the same temporal frequency power spectra as the moving inducer but induced no illusory motion.



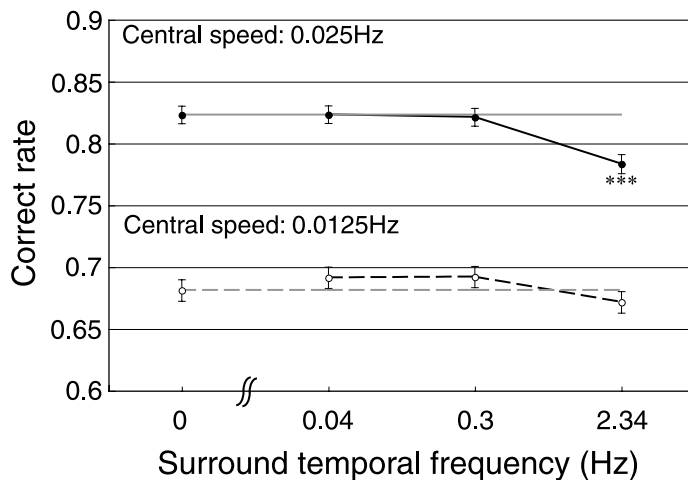


Figure 5. Results of under the control condition using a counter-phase flicker. The abscissa indicates the temporal frequency of the surrounding stimulus. Other conventions are identical to those used in Figure 4.

Figure 5 shows the results in the case of surround counter-phase flicker. We compared the detection performance across surround temporal frequencies. At a higher temporal frequency, the correct response rate was either degraded (two-tailed  $z$ -test,  $p < 0.001$ ) or unaffected, as in the case of the moving inducer. However, unlike the results for the moving inducer, neither enhancement nor degradation of detection performance was observed at intermediate temporal frequencies. Thus, a higher temporal frequency of the surround can degrade the motion detection sensitivity of the central stimulus, but the enhancement of sensitivity observed at the intermediate speeds of the moving inducer cannot be explained by the effect of the temporal frequency of the surround.

## Discussion

### The importance of the later stage in visual motion detection

In Experiment 1, we found that the perceived motion direction of the central stimulus was biased toward the direction of illusory motion induced by surrounding motion, suggesting that physical and induced motion components can be integrated. In Experiment 2, we found that motion detection sensitivity for central horizontal motion was enhanced by the presence of surrounding motion at a moderate speed compared with a stationary surround condition. We confirmed this effect could not be explained by the temporal frequency component in the surround because we found no enhancement of motion detection sensitivity in the presence of surrounding

counter-phase flicker. To summarize, the results of the present study indicate that motion detection sensitivity for central horizontal motion changes according to the change of perceived direction resulting from the influence of induced motion. Although a previous study reported that orientation-discrimination performance was enhanced by orthogonal orientation signals (Clifford, Wyatt, Arnold, Smith, & Wenderoth, 2001), our finding, suggesting that orthogonal illusory motion enhances motion detection sensitivity, is new.

These results support the idea that the later, global motion processing stage is critical for determining the perceptual limit of motion detection because even though the motion information of the central patch was totally equivalent across conditions, motion detection sensitivity changed depending on the outcome of complex information processing such as motion integration, the solution of the aperture problem, and center-surround interactions. This stage may be mainly mediated by area MT and later cortical areas such as MSTl, where global motion information is represented and the center-surround antagonism is frequently found (Allman et al., 1985; Castelo-Branco et al., 2002; Eifuku & Wurtz, 1998; Huk & Heeger, 2002; Movshon & Newsome, 1996; Perge et al., 2002; Rodman & Albright, 1989).

### A model to explain the enhancement and degradation of motion detection sensitivity

Why does integration with the illusory motion component enhance sensitivity? We propose that this enhancement is the outcome of interactions among visual signals and two types of internal noise in the human brain: a speed noise and a directional noise.

The visual system has both speed tuning and directional selectivity (Cheng, Hasegawa, Saleem, & Tanaka, 1994; Maunsell & Van Essen, 1983), and classical as well as recent psychophysical studies have reported that speed and direction representations are processed independently (Ball & Sekuler, 1980; Hol & Treue, 2001).

On the basis of these ideas, we propose a simple model to explain our experimental results, in which the internal signal of visual motion is faithfully represented in the visual system in polar coordinates, the direction indicates the direction of motion represented, and the distance from the origin indicates the speed (Figure 6).

Under the stationary-surround condition, the central motion appears to be purely horizontal but extremely slow. Although the direction representation in the visual system has a suitable shape (i.e., exactly left versus exactly right), the speed representation in regard to whether the stimulus is moving as opposed to stationary is within the area of internal speed noise (gray circle, Figure 6) and cannot reliably convey the characteristics of the motion. When the inducer moves very fast, its high

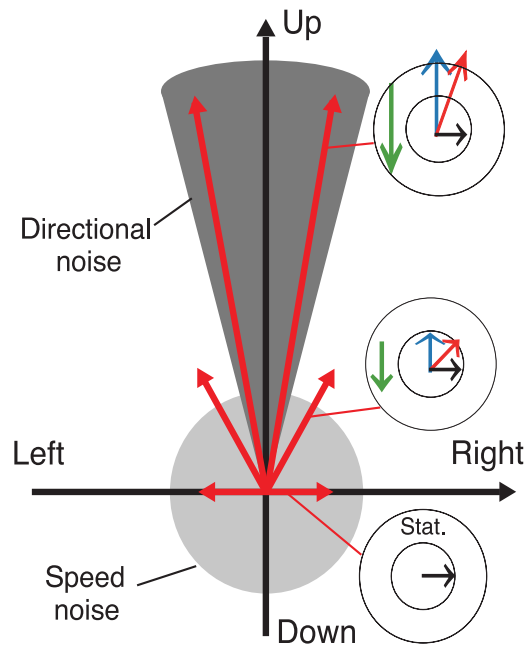


Figure 6. A model of visual-motion representation that explains the enhancement and degradation of detection sensitivity by induced motion. The internal noise for speed-limiting minimum-motion sensitivity is indicated schematically by the gray circle, whereas the internal noise for direction-limiting direction discriminability is indicated by the dark gray arc. For illustrative purposes, signals within the area of speed noise are assumed to be indistinguishable from a speed of zero, and signals within the area of directional noise are assumed to be indistinguishable from vertical, although bell-shaped functions such as Gaussian functions would be more realistic from a biological perspective.

temporal frequency tends to mask visual events in the center. Even if the masking were not intense, the detection task should suffer from the directional noise we tentatively included as a factor in our model. The central motion appears to move rapidly in the induced vertical direction, but in almost the same direction irrespective of whether the motion is physically to the left or right. As mentioned in previous studies (Jazayeri & Movshon, 2006, 2007), subjects were required to perform fine direction discrimination under this condition, in that they were asked to discriminate two slightly oblique directions (e.g., 80 deg versus 100 deg). Under such circumstances, task difficulty is different from that found under coarse direction discrimination conditions for horizontally perceived motion (e.g., 0 deg versus 180 deg). Although the speed is sufficiently high, the direction representation is not a reliable cue for discriminating between the two oblique directions, both of which are almost vertical and within the area of internal directional noise (gray arc in Figure 6). When inducer speed is optimal, both the speed representation and the direction representation convey accurate information because the represented motion escapes from

both speed and direction noises, and motion detection is enhanced.

### Effect of vertical induced motion on perceived direction of horizontal motion

The results of Experiment 1 confirmed that induced motion and physical motion were integrated, as shown in Figure 2, and that the subsequent perceived direction depended on the speeds of the inducer and the central patch.

In previous psychophysical studies, Gogel (1979) used point-light stimuli and showed that physical motion and induced motion could be integrated and that the perceived direction depended on the speeds of the inducer and the central patch. Kim and Wilson (1997) used sinusoidal gratings presented in the center and surround. They also showed that the perceived motion direction of the central stimulus was biased toward the direction opposite to that of the surrounding motion. The present results are consistent with the results of these studies.

More interestingly, our results suggest the possibility that induced motion constrains the solution to the aperture problem. When presented alone, the Gabor patch appeared to move orthogonally to the grating pattern; theoretically, however, the true motion direction could be toward any point along a constraint line (Hildreth, 1984). The perceptual influence of the surrounding inducer may override the preference for slower velocities (Weiss, Simoncelli, & Adelson, 2002) and may bias the solution to the aperture problem toward the direction of induced motion. We informally observed that when the inducer moved faster, the perceived direction was more oblique and the perceived speed of the central grating increased.

Although physiological studies examining the integration between physical and induced motions are limited, area MT and higher cortical sites are likely candidates for relevant mechanisms mediating this phenomenon because area MT contains neurons that exhibit surround-suppression properties (Allman et al., 1985; Eifuku & Wurtz, 1998; Perge et al., 2002), neurons that show directional tuning to pattern motion (Castelo-Branco et al., 2002; Huk & Heeger, 2002; Movshon & Newsome, 1996; Rodman & Albright, 1989), and neurons that seem to be involved in the solution of the aperture problem (Pack & Born, 2001). Although the center-surround antagonism with respect to motion direction is also found in the primary visual cortex (Jones, Grieve, Wang, & Sillito, 2001), our induced motion is more likely to be attributable to neuronal activities in extrastriate areas such as area MT because, during the course of stimulus optimization, we observed the maximal induced motion when the size of the central stimulus was compatible with the average size of the classical receptive fields of neurons in area MT. Previous psychophysical studies have already shown that

induced motion tends to occur more vigorously with larger stimulus sizes that are similar to the size of the receptive fields of area MT neurons (Murakami & Shimojo, 1993, 1996).

## Implications of motion detection sensitivity enhancement

Our findings also reveal the intriguing possibility that the perception of illusory motion maximizes motion detection, indicating that humans can render their sensory systems supersensitive by using normally unused information, such as early-stage visual representations of the horizontal slow physical motion component in our experiment. The human visual system does not utilize every kind of information that depicts a tiny change and is actually registered in earlier cortical representations. Rather, in normal circumstances, our vision works by prohibiting access to information that could impair the stability and constancy of the visual world. The visual system interprets the visual world as appearing in a “default” condition (e.g., a stationary and complete world) even though local input signals sometimes suggest the contrary (Morgan, Chubb, & Solomon, 2008; Ross & Burr, 2008). For example, small eye movements occur incessantly, and resulting retinal image motions are registered in early visual representations (Snodderly, Kagan, & Gur, 2001), but we normally see a stationary world as stationary (Murakami, 2003; Murakami & Cavanagh, 1998, 2001; Sasaki et al., 2002). Another example is the blind spot: although the primary visual area has a cortical region that corresponds to the blind spot lacking visual responsiveness (Fiorani, Rosa, Gattas, & Rocha-Miranda, 1992), we normally perceive continuous lines and surfaces filling in the blind spot. Our results indicate, however, that the visual system can use such early signals efficiently to maximize performance if they are integrated with other visual codes, thus producing a new internal representation, one that is most appropriate for accomplishing the perceptual task in question (e.g., a minimum-motion detection task).

## Conclusions

We conclude that detection performance for slow horizontal motion within a frame of reference can be enhanced by a vertical illusory motion induced by surrounding motion. The effect depends on inducer speed, not temporal frequency. Our findings suggest that the later-stage processing, in which multiple motion signals are integrated, is critical for reaching the human perceptual limit of minimum-motion detection.

## Acknowledgments

We thank Masato Okada and Satohiro Tajima for critical discussions and reading this manuscript. This research was supported by the Nissan Science Foundation.

Commercial relationships: none.

Corresponding author: Hiromasa Takemura.

Email: hiromasa@fechner.c.u-tokyo.ac.jp.

Address: 3-8-1, Komaba, Meguro-ku, Tokyo, Japan.

## References

- Adelson, E. H., & Movshon, J. A. (1982). Phenomenal coherence of moving visual patterns. *Nature*, *300*, 523–525. [PubMed]
- Allman, J., Miezin, F., & McGuinness, E. (1985). Direction- and velocity-specific responses from beyond the classical receptive field in the middle temporal visual area (MT). *Perception*, *14*, 105–126. [PubMed]
- Ball, K., & Sekuler, R. (1980). Models of stimulus uncertainty in motion perception. *Psychological Review*, *87*, 435–469. [PubMed]
- Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, *10*, 433–436. [PubMed]
- Britten, K. H., Newsome, W. T., Shadlen, M. N., Celebrini, S., & Movshon, J. A. (1996). A relationship between behavioral choice and the visual responses of neurons in macaque MT. *Visual Neuroscience*, *13*, 87–100. [PubMed]
- Castelo-Branco, M., Formisano, E., Backes, W., Zanella, F., Neuenschwander, S., Singer, W., et al. (2002). Activity patterns in human motion-sensitive areas depend on the interpretation of global motion. *Proceedings of the National Academy of Sciences of the United States of America*, *99*, 13914–13919. [PubMed] [Article]
- Cheng, K., Hasegawa, T., Saleem, K. S., & Tanaka, K. (1994). Comparison of neuronal selectivity for stimulus speed, length, and contrast in the prestriate visual cortical areas V4 and MT of the macaque monkey. *Journal of Neurophysiology*, *71*, 2269–2280. [PubMed]
- Clifford, C. W., Wyatt, A. M., Arnold, D. H., Smith, S. T., & Wenderoth, P. (2001). Orthogonal adaptation improves orientation discrimination. *Vision Research*, *41*, 151–159. [PubMed]
- Derrington, A. M., & Badcock, D. R. (1992). Two-stage analysis of the motion of 2-dimensional patterns: What is the first stage? *Vision Research*, *32*, 691–698. [PubMed]



- Derrington, A., & Suero, M. (1991). Motion of complex patterns is computed from the perceived motions of their components. *Vision Research*, *31*, 139–149. [PubMed]
- Ditterich, J., Mazurek, M. E., & Shadlen, M. N. (2003). Microstimulation of visual cortex affects the speed of perceptual decisions. *Nature Neuroscience*, *6*, 891–898. [PubMed]
- Duncker, L. (1929). Über induzierte Bewegung. *Psychologische Forschung*, *12*, 180–259. In W. D. Ellis (Ed. & Trans.) *Source book of Gestalt psychology* (1950) (pp. 161–172). London: Kegan Paul, Trench, Trubner & Co.
- Eifuku, S., & Wurtz, R. H. (1998). Response to motion in extrastriate area MSTl: Center–surround interactions. *Journal of Neurophysiology*, *80*, 282–296. [PubMed] [Article]
- Fiorani, M., Rosa, M. G. P., Gattas, R., & Rocha-Miranda, C. E. (1992). Dynamic surrounds of receptive fields in primate striate cortex: A physiological basis for perceptual completion? *Proceedings of the National Academy of Sciences of the United States of America*, *89*, 8547–8551. [PubMed]
- Gogel, W. C. (1979). Induced motion as a function of the speed of the inducing object, measured by means of two methods. *Perception*, *8*, 255–262. [PubMed]
- Hildreth, H. (1984). *The measurement of visual motion*. Cambridge, MA: MIT Press.
- Hol, K., & Treue, S. (2001). Different populations of neurons contribute to the detection and discrimination of visual motion. *Vision Research*, *41*, 685–689. [PubMed]
- Huk, A. C., & Heeger, D. J. (2002). Pattern-motion responses in human visual cortex. *Nature Neuroscience*, *5*, 72–75. [PubMed]
- Jazayeri, M., & Movshon, J. A. (2006). Optimal representation of sensory information by neural populations. *Nature Neuroscience*, *9*, 690–696. [PubMed]
- Jazayeri, M., & Movshon, J. A. (2007). Integration of sensory evidence in motion discrimination. *Journal of Vision*, *7*(12):7, 1–7, <http://journalofvision.org/7/12/7/>, doi:10.1167/7.12.7. [PubMed] [Article]
- Jones, H. E., Grieve, K. L., Wang, W., & Sillito, A. M. (2001). Surround suppression in primate V1. *Journal of Neurophysiology*, *86*, 2011–2028. [PubMed] [Article]
- Kim, J., & Wilson, H. R. (1997). Motion integration over space: Integration of the center and surround motion. *Vision Research*, *37*, 991–1005. [PubMed]
- Legge, G. E., & Campbell, F. W. (1981). Displacement detection in human vision. *Vision Research*, *21*, 205–213. [PubMed]
- Maunsell, J. H. R., & Van Essen, D. C. (1983). Functional properties of neurons in middle temporal visual area of macaque monkeys: I. Selectivity for stimulus direction, speed, and orientation. *Journal of Neurophysiology*, *49*, 1127–1147. [PubMed]
- McKee, S. P., & Nakayama, K. (1984). The detection of motion in the peripheral visual field. *Vision Research*, *24*, 25–32. [PubMed]
- Morgan, M., Chubb, C., & Solomon, J. A. (2008). A ‘dipper’ function for texture discrimination based on orientation variance. *Journal of Vision*, *8*(11):9, 1–8, <http://journalofvision.org/8/11/9/>, doi:10.1167/8.11.9. [PubMed] [Article]
- Movshon, J. A., & Newsome, W. T. (1996). Visual response properties of striate cortical neurons projecting to area MT in macaque monkeys. *The Journal of Neuroscience*, *16*, 7733–7741. [PubMed] [Article]
- Murakami, I. (2003). Illusory jitter in a static stimulus surrounded by a synchronously flickering pattern. *Vision Research*, *43*, 957–969. [PubMed]
- Murakami, I. (2004). Correlations between fixation stability and visual motion sensitivity. *Vision Research*, *44*, 751–761. [PubMed]
- Murakami, I., & Cavanagh, P. (1998). A jitter after-effect reveals motion-based stabilization of vision. *Nature*, *395*, 798–801. [PubMed]
- Murakami, I., & Cavanagh, P. (2001). Visual jitter: Evidence for visual-motion-based compensation of retinal slip due to small eye movements. *Vision Research*, *41*, 173–186. [PubMed]
- Murakami, I., & Shimojo, S. (1993). Motion capture changes to induced motion at higher luminance contrasts, smaller eccentricities, and larger inducer sizes. *Vision Research*, *33*, 2091–2107. [PubMed]
- Murakami, I., & Shimojo, S. (1996). Assimilation-type and contrast-type bias of motion induced by the surround in a random-dot display: Evidence for center–surround antagonism. *Vision Research*, *36*, 3629–3639. [PubMed]
- Newsome, W. T., Britten, K. H., & Movshon, J. A. (1989). Neuronal correlates of a perceptual decision. *Nature*, *341*, 52–54. [PubMed]
- Pack, C. C., & Born, R. T. (2001). Temporal dynamics of a neural solution to the aperture problem in visual area MT of macaque brain. *Nature*, *409*, 1040–1042. [PubMed]
- Pelli, D. G. (1997). The videotoolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, *10*, 437–442. [PubMed]
- Perge, J. A., Borghuis, B. G., Bours, R. J. E., Lankheet, M. J. M., & van Wezel, R. J. A. (2002). Dynamics of directional selectivity in MT receptive field centre



- and surround. *The European Journal of Neuroscience*, 22, 2049–2058. [PubMed]
- Reinhardt-Rutland, A. H. (1988). Induced movement in the visual modality: An overview. *Psychological Bulletin*, 103, 57–71. [PubMed]
- Rodman, H. R., & Albright, T. D. (1989). Single-unit analysis of pattern-motion selective properties in the middle temporal visual area (MT). *Experimental Brain Research*, 75, 53–64. [PubMed]
- Ross, J., & Burr, D. (2008). The knowing visual self. *Trends in Cognitive Sciences*, 12, 363–364. [PubMed]
- Salzman, C. D., Murasugi, C. M., Britten, K. H., & Newsome, W. T. (1992). Microstimulation in visual area MT: Effects on direction discrimination performance. *The Journal of Neuroscience*, 12, 2331–2355. [PubMed] [Article]
- Sasaki, Y., Murakami, I., Cavanagh, P., & Tootell, R. H. B. (2002). Human brain activity during illusory visual jitter as revealed by functional magnetic resonance imaging. *Neuron*, 35, 1147–1156. [PubMed]
- Serences, J. T., & Boynton, G. M. (2007). The representation of behavioural choice for motion in human visual cortex. *The Journal of Neuroscience*, 27, 12893–12899. [PubMed] [Article]
- Shioiri, S., Ito, S., Sakurai, K., & Yaguchi, H. (2002). Detection of relative and uniform motion. *Journal of the Optical Society of America A, Optics, Image Science, and Vision*, 19, 2169–2179. [PubMed]
- Simoncelli, E. P., & Heeger, D. J. (1998). A model of neuronal responses in visual area MT. *Vision Research*, 38, 743–761. [PubMed]
- Snodderly, D. M., Kagan, I., & Gur, M. (2001). Selective activation of visual cortex neurons by fixational eye movements: Implications for neural coding. *Visual Neuroscience*, 18, 259–277. [PubMed]
- Stone, L. S., Watson, A. B., & Mulligan, J. B. (1990). Effect of contrast on the perceived direction of a moving plaid. *Vision Research*, 30, 1049–1067. [PubMed]
- Tadin, D., Lappin, J. S., Gilroy, L. A., & Blake, R. (2003). Perceptual consequences of centre-surround antagonism in visual motion processing. *Nature*, 424, 312–315. [PubMed]
- Takeuchi, T., & De Valois, K. K. (2000). Modulation of perceived contrast by a moving surround. *Vision Research*, 40, 2697–2709. [PubMed]
- Tyler, C. W., & Torres, J. (1972). Frequency response characteristics for sinusoidal movement in the fovea and periphery. *Perception & Psychophysics*, 12, 232–236.
- Weiss, Y., Simoncelli, E. P., & Adelson, E. H. (2002). Motion illusions as optimal percepts. *Nature Neuroscience*, 5, 598–604. [PubMed]
- Welch, L. (1989). The perception of moving plaids reveals two motion-processing stages. *Nature*, 337, 734–736. [PubMed]
- Wilson, H. R., Ferrera, V. P., & Yo, C. (1992). A psychophysically motivated model for two-dimensional motion perception. *Visual Neuroscience*, 9, 79–97. [PubMed]