Surround facilitation for rapid motion perception

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Because we live in a dynamic environment with moving eyes and body, our retinas are often stimulated by new scenes that appear suddenly and are only briefly available. How the visual system successfully extracts information from such challenging stimulation is not yet understood. For some stimuli, like photos of natural scenes, we are accurate in detecting objects like animals or faces even when the stimulus is presented for a short time. For other stimuli, like noisy motion, previous studies have shown accurate perception only when the stimulus is presented for a long time — often longer than the typical available time of a stimulus in natural viewing. Here we show, however, that a transient surround can accelerate the perception of motion. We found that for briefly displayed random-dots, the signal necessary to detect motion is reduced from 19% to 8% when a task-irrelevant surround is presented in synchrony with the random-dots, while no improvement occurs when the surround is sustainedly presented, or when it is transiently, but asynchronously, presented. We also found that motion sensitivity increases steadily with duration when no surround is presented, confirming previous findings, but duration has little effect on sensitivity when a synchronous surround is presented. Further results indicate that the facilitation by a synchronous surround is related to relative-motion processing. Our findings suggest that spatial interactions might assist rapid perception of motion.

Keywords: motion-2D, motion integration, center-surround interactions

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Introduction

As we are organisms with moving eyes, heads, and bodies, our retinas are often stimulated by new scenes that appear suddenly and are only briefly available. Abrupt changes in the retinal image also occur when a sudden change happens in the environment, which is common in emergencies. Thus, it is biologically advantageous to accurately perceive new stimuli that are accessible for a short time.

Perception of brief stimuli is computationally challenging because, in comparison with longer stimuli, brief stimuli carry less sensory information and are more likely to be masked by irrelevant stimuli presented immediately before or after (Macknik & Livingstone, 1998). How the visual system maintains accurate perception for stimuli that last for a short time is not yet understood. Behavioral studies have shown very fast perceptual decisions about contrast (Ludwig et al., 2005), color (Stanford et al., 2010), and complex objects like photos of animals or faces (Crouzet, Kirchner, & Thorpe, 2010; Keysers et al., 2001; Kirchner & Thorpe, 2006). Furthermore, neurophysiologic studies have shown that many visual neurons respond vigorously to stimulus onset and much of the information is encoded in this early response (Buracas et al., 1998; Chen, Geisler & Seidemann, 2008; Ghose & Harrison, 2009; Keysers et al., 2001; Muller et al., 2001; Osborne, Bialek & Lisberger, 2004; Uka & DeAngelis, 2003). These findings not only indicate that visual processing is faster than previously thought, but also suggest that information does not need to be integrated over a long time before reaching a perceptual judgment.

It is also known, however, that for visual motion perception, brief stimulus presentation degrades perception when the signal is weak and the noise is strong. A well-studied example is the detection of motion signal in a display of dynamic random-dots (Barlow & Tripathy, 1997; Downing & Movshon, 1989; Morgan &

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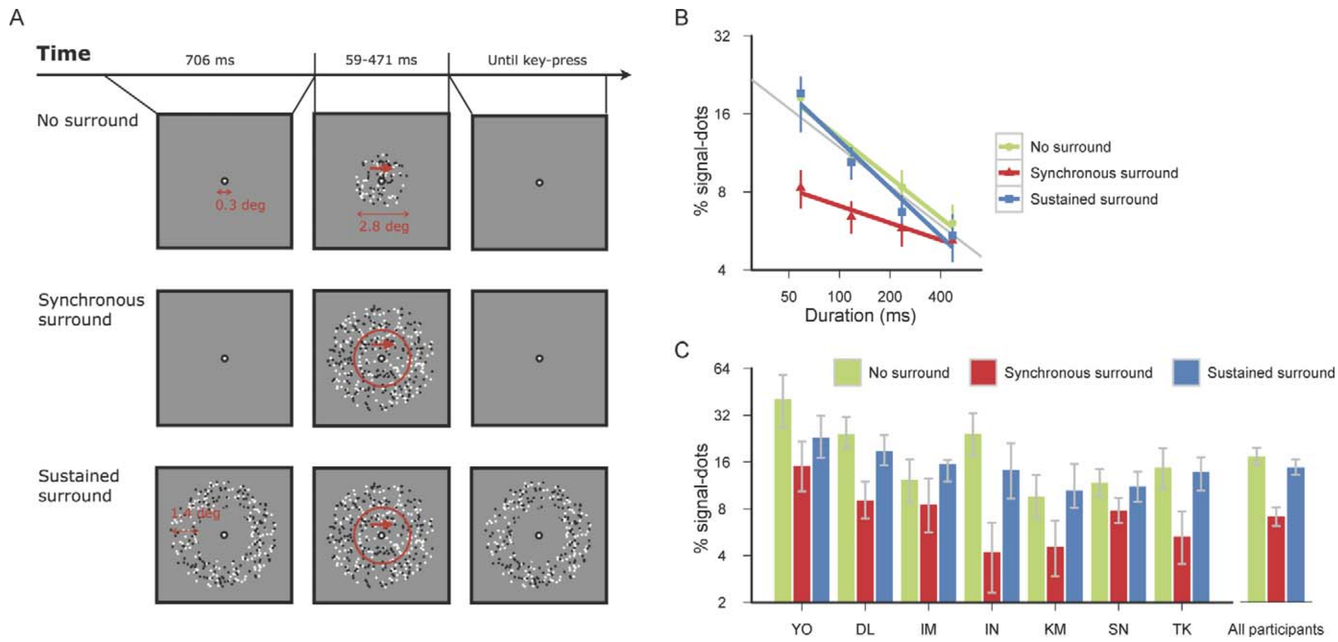

Figure 1. (A), Schematic illustration of the stimuli for Experiment 1. Everything depicted in red was not displayed in the experiment. In both surround conditions, the dots in the surround were static. (B), Signal necessary to discriminate motion direction as a function of the duration of the motion target for Experiment 1. Each data point shows the signal threshold averaged across observers. The colored lines show linear regression fits. A grey line with slope −0.5 in log-log axis is plotted for comparison. The error bars correspond to the 95% bootstrap confidence intervals (see Methods section of Experiment 1). (C), Signal necessary to discriminate motion direction for each observer, and average across observers, for the shortest motion target presentation (59 ms) in Experiment 1. The individual error bars shows the 95% bootstrap confidence intervals (Foster & Bischof, 1997). The error bars for the averaged thresholds correspond to the 95% bootstrap confidence intervals (see General Methods section).

Ward, 1980; Newsome & Paré, 1988; Williams & Sekuler, 1984). In this task, when the stimulus duration is reduced, motion detection sensitivity rapidly decreases according to a prediction based on the reduction of available sensory samples (Barlow & Tripathy, 1997; Downing & Movshon, 1989; Gold & Shadlen, 2007; Kiani, Hanks, & Shadlen, 2008). This suggests that the visual system needs to integrate noisy motion over a long time to accumulate sufficient signal for detection, which compromises the perception of briefly presented stimuli such as those found in natural conditions. We found, however, that motion signal is extracted very rapidly from a noisy motion stimulus when a task-irrelevant surround is presented in synchrony with the motion stimulus, suggesting that spatial interactions are important for rapid perception of motion.

General methods

Stimuli were generated using PsychoPy (Peirce, 2007) and displayed on a monitor (GDM-F520, SONY, Tokyo) at a refresh rate of 85 Hz (800 × 600 pixels). Observers viewed the display from a distance of 90 cm in a dimly lit room while fixating a small black ring (0.3° of diameter) in the center of the screen. The experiments were approved by the NTT Communication Science Laboratories Research Ethics Committee and were conducted in accordance with the Declaration of Helsinki.

Experiment 1: A synchronous surround enhances detection of brief motion pulses

Using a display of random dots (Downing & Movshon, 1989; Newsome & Paré, 1988; Figure 1A), we measured motion sensitivity as a function of the duration of the stimulus for three conditions: no surround, synchronous surround and sustained surround.

Methods

The motion target was presented 706 ms after the onset of each trial. It consisted of 100 dots of diameter 0.1° displayed within a circular aperture in a grey background (29 cd/m^2) for different durations (59 ms, 118 ms, 235 ms and 471 ms). Half of the dots were black (4 cd/m^2) and half were white (62 cd/m^2). The life-time and the speed of the signal-dots were four frames and 7.84°/s, respectively. The life-time of the noise-dots was one frame (11.7 ms). In each presentation, some of the dots (signal) moved to the left or to the right while the remaining dots (noise) randomly changed position. We estimated motion sensitivity as the minimum proportion of signal-dots needed for the observers to detect the correct direction of motion. In the synchronous surround condition, a surrounding ring composed of static dots with the same density as the motion target was displayed simultaneously with the motion target. In the sustained surround condition, the surrounding ring was displayed from the onset of the trial and remained on the screen until observers responded. Different surround conditions and durations were tested in different blocks of trials. Within a block, the number of signal-dots was varied in each trial according to the method of constant stimuli. The spatial dimensions of the elements composing the stimulus are displayed in Figure 1.

Four observers—two authors and two observers that did not know the experimental hypotheses—were tested using all the durations of the motion target. Three more observers (one author) were only tested for the shortest duration of the stimuli (59 ms). For each observer, the proportions of correct responses as a function of the number of signal-dots were fitted with logistic functions estimated by maximizing the log-likelihood. Thresholds were estimated as the signal necessary to correctly discriminate motion direction 75% of the time. Individual confidence intervals were obtained by bootstrap (Foster & Bischof, 1997). The confidence intervals for the averaged thresholds were obtained as follow. For each observer, a bootstrap sample was obtained. These samples were then averaged across observers to obtain a sampled average threshold. A thousand sampled average thresholds were calculated in this way. The confidence intervals were estimated using the 5% and 95% percentiles. Each observer performed approximately 4,000 trials.

Results and discussion

When the random-dots were presented in isolation (Figure 1A, no surround condition), the signal necessary to discriminate motion increased as the presentation time of the random-dots was shortened (Figure 1B, green circles). The decrease in motion sensitivity as the duration of the stimulus was reduced confirms previous results obtained with humans (Barlow & Tripathy, 1997; Burr & Santoro, 2001; Downing & Movshon, 1989; Festa & Welch, 1997; Selen, Shadlen & Wolpert, 2012; Watamaniuk & Sekuler, 1992; Watamaniuk, Sekuler, & Williams, 1989) and monkeys (Britten et al., 1992; Gold & Shadlen, 2007; Kiani et al., 2008). Quantitatively, motion sensitivity declined as the square-root of duration (slope about –0.5 on log-log axis), which also confirms previous findings (Barlow & Tripathy, 1997; Downing & Movshon, 1989; Gold & Shadlen, 2007; Kiani et al., 2008; also see Burr & Santoro, 2001) and is consistent with perfect combination of statistical independent samples (Barlow & Tripathy, 1997; Downing & Movshon, 1989; Gold & Shadlen, 2007; Kiani et al., 2008).

For the longest stimulus (471 ms), observers only needed 6% of signal-dots (average) to discriminate motion (Figure 1B, most rightwards green circle). Other studies have shown that even weaker signals are still detected when the stimulus lasts for seconds (e.g., Burr & Santoro, 2001; Newsome & Paré, 1988). For the shortest stimulus (59 ms), observers needed much more signal-dots (19%) to discriminate motion (Figure 1B, most leftwards green circle). We found, however, that this relatively poor sensitivity for brief motion pulses was greatly enhanced when we presented, in synchrony with the motion target, a task-irrelevant surround composed of static random dots (Figure 1A, synchronous surround condition). Observers only needed 8% signal at the shortest duration of 59 ms (Figure 1B, most leftwards red triangle). This high sensitivity improved little with further exposure of the stimulus (Figure 1B, red line) so that for the 471 ms motion target, sensitivity using a synchronous surround was the same as that with any surround.

It could be argued that the surround facilitation we found is caused by the addition of a static spatial reference. To test this possibility, we presented the surround well before the motion pulse and removed it well after (Figure 1A, sustained surround condition). In this situation, the spatial structure of the stimulus during the motion pulse was identical to the synchronous surround condition. The static surround could provide spatial references in both cases. The only difference is the temporal context: in the sustained surround condition, the onset and the offset of the surround were separated from the onset and offset of the motion target. We did not find surround facilitation for the sustained presentation of the surround (Figure 1B, blue squares), which indicates that the enhancement effect is not related to spatial referencing.

For three more observers, we confirmed the surround facilitation of motion for the 59-ms motion pulse using a synchronous surround (Figure 1C shows the results for the seven observers). We also confirmed that the surround facilitation occurred for a motion target containing a different type of random-dot stimulus, in which the noise-dots moved in random directions with the same life-time as the signal-dots. With this directional noise, the signal-dots necessary for detection of motion in the 59 ms pulse was 17% (CI, 15% to 19%)

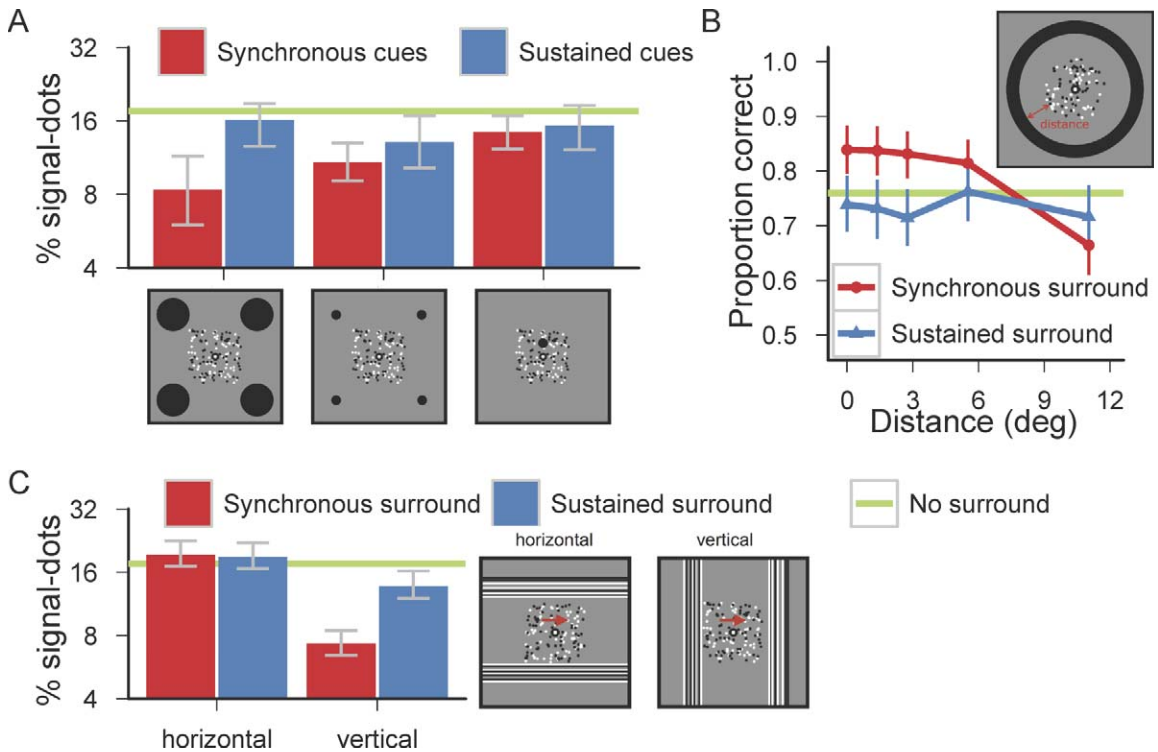

Figure 2. (A), Signal necessary to discriminate motion direction averaged across observers for several types of cues (Experiment 3). The error bars for the averaged thresholds correspond to the 95% bootstrap confidence intervals (see Methods of Experiment 3). (B), Proportion of correct direction discriminations averaged across observers as a function of the separation between the motion target and a task-irrelevant surrounding ring for both synchronous and sustained ring presentations (Experiment 2). The green horizontal line shows the proportion of correct discriminations without any surround. The error bars for the averaged thresholds correspond to the 95% bootstrap confidence intervals (see Methods of Experiment 2). (C), Signal necessary to discriminate motion direction averaged across observers for Experiment 4. The green horizontal line shows the average across observers when no surround was displayed. The error bars for the averaged thresholds correspond to the 95% bootstrap confidence intervals (see Methods section of Experiment 4).

for the *No surround condition*, 10% (CI, 9% to 11%) for the *Synchronous surround condition* and 14% (CI, 13% to 16%) for the *Sustained surround condition* (average of seven observers). This result suggests that the mechanism of enhancement does not discriminate signal and noise dots based on life-time (see General Discussion).

Experiment 2: The surround should not be displayed very far away from the motion target

To examine the spatial range of the surround facilitation, we manipulated the separation between the motion target and a surround that, in this experiment, was a black uniform ring (Figure 2B).

Methods

The motion target was presented 706 ms after the onset of each trial for 59 ms. The width of the surrounding black ring was 1.4° and the luminance 12 cd/m^2. Synchronous, sustained, and no surrounds were tested in different blocks of trials. The distance was randomized within each block. The percentage of signal was fixed individually for each observer to obtain around 75% of correct responses when no cues were displayed. The confidence intervals for the proportion correct were obtained as follows. For each observer, a bootstrap sample of the correct responses was obtained. These samples were then averaged across observers to obtain a sampled average of the correct responses. A thousand samples were calculated in this way. The confidence intervals were estimated using the 5% and 95% percentiles. Each of the four observers (including two of the authors) performed approximately 1,000 trials.

Results and discussion

Surround facilitation occurred not only when the surrounding ring was abutting the target, but also for fairly large separations up to about 6° (Figure 2B; in this experiment we fixed the amount of signal and measured the proportion of correct direction discriminations). For the largest separation that we tested (~11°), the synchronous surround slightly impaired, rather than facilitated, motion perception.

Experiment 3: Effects of other visual cues

In Experiment 2, we showed that motion is enhanced not only with static dots in the surround but also with a uniform ring, which indicates that surround facilitation is not sensitive to the pattern similarity between the center and the surround. In this experiment, we tested other task-irrelevant cues (Figure 2A).

Methods

The motion target was presented 706 ms after the onset of each trial for 59 ms. All the cues were black (4 cd/m^2). The large discs had a diameter of 1.8° and their centers were separated 2.3° from fixation. The small discs had a diameter of 0.3° and their centers were separated 2.3° from fixation. The small dot had a diameter of 0.3° and was presented 1.4° above fixation. Five observers (including two authors) were tested using the cues just described. In this experiment, we did not collect data for the no-surround condition. Four of the five participants, however, also participated in Experiment 4 for which we have data for the no-surround condition. Hence, we replotted in Figure 2A the base-line in Figure 2C corresponding to the no-surround condition. Motion sensitivity was also tested in three observers (two authors) using static black and white random dots as task-irrelevant cues. The dots were presented within the region of the motion target (the dot density was the same as that of the static dots in the surround). The confidence intervals were obtained as in Experiment 1. Each observer performed approximately 3,000 trials.

Results and discussion

Sensitivity was enhanced when the motion target was surrounded by four surrounding large discs (Figure 2A), indicating that closure of the surround is not necessary to obtain the effect. Sensitivity was not enhanced, however, when we severely reduced the size of the four discs into four dots, or when the cue was a small dot displayed above fixation (Figure 2A). A follow-up experiment further showed no sensitivity enhancement when static random dots were presented within the region of the motion target — the average signal to discriminate motion direction was 22% (CI, 17% to 26%) for the *Synchronous surround condition* and 21% (CI, 17% to 24%) for the *Sustained surround condition*. These findings suggest that a relatively large area of the surround needs to be stimulated.

Experiment 4: The orientation of the surround should be orthogonal to the direction of motion

We have shown that large surrounds that are displayed in synchrony with the motion target, but not very far from it, boost motion sensitivity. We hypothesized that the surround facilitation might be related to the processing of direction-selective neurons with center-surround structure, which are found in many stages of visual motion processing (Allman, Miezin, & McGuinness, 1985), and are associated with the computation of relative motion (Loomis & Nakayama, 1973). If the surround facilitation is related to relative-motion processing, then a surround that does not facilitate the computation of relative motion, even if large, will not cause surround facilitation. To test that, we used two types of surrounds: horizontal and vertical (Figure 2C). The *horizontal surround* was composed of two bands of horizontal random-lines, one above and the other below the target motion. In the *vertical surround*, the random-lines were vertical and presented on the left and right of the target. Because the direction of the target motion was horizontal (left or right), the 'horizontal surround' precludes relative motion processing — assuming that the extremes of the random-lines are not used.

Methods

The motion target was presented 706 ms after the onset of each trial for 59 ms. The random-dots were placed within a square aperture (size: 2.8°). Each surround was composed of two sets of random-bars. Each set had 20 black (4 cd/m^2) and 20 white bars (62 cd/m^2) positioned randomly within an area of width 1.4°. The size of each bar was 0.1° by 18°. Each type of surround was tested in different blocks of trials. The confidence intervals were obtained as in Experiment 1. Each of the four observers (including two authors) performed approximately 2,000 trials.

Results and discussion

Consistent with the involvement of relative motion processing, motion sensitivity was not enhanced by the

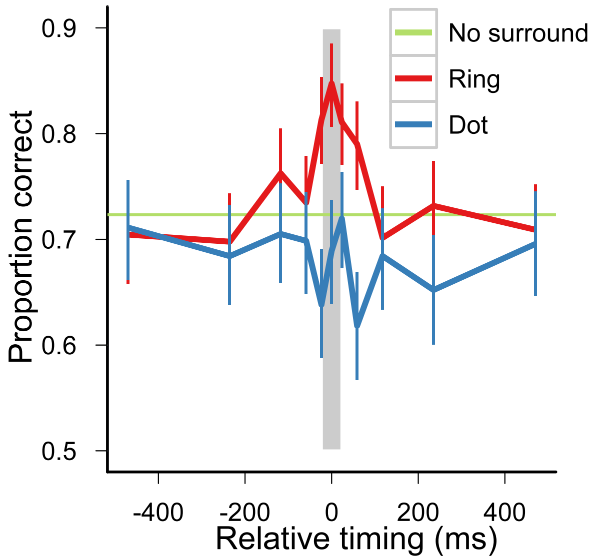

Figure 3. Proportion of correct direction discriminations averaged across observers as a function of the relative timing between the motion target and two types of visual cues (Experiment 5). The green horizontal line shows the average across observers when no cues were displayed. Negative relative timings indicate that the cue was presented before the motion target. The error bars for the averaged thresholds correspond to the 95% bootstrap confidence intervals (see Methods section of Experiment 5).

synchronous presentation of the horizontal surround (Figure 2C). For the vertical surround, however, we found a surround facilitation similar to that found with the other large surrounds that we tested.

Experiment 5: Transient surrounds should be presented in synchrony

The final experiment examined the temporal tuning of the surround enhancement.

Methods

We tested the temporal tuning of the surround facilitation by presenting a black ring (width: 1.4°, luminance: 12 cd/m^2) at different timings. For comparison, we also tested the temporal tuning using a dot of 0.3° of diameter displayed 1.4° above fixation. The percentage of signal was fixed individually for each observer to obtain around 75% of correct responses when no cues were displayed. Different cues were tested in different blocks of trials. The relative timing was randomized within each block. The confidence intervals were obtained as in Experiment 2. Each of four observers (including two authors) performed approximately 2,000 trials.

Results and discussion

When we presented a ring surrounding the motion target at different timings relative to the motion target, we found that sensitivity was only enhanced for timings around the synchronous presentation (red lines in Figure 3). Regardless of the cue timing, sensitivity was not enhanced by the single-dot cue (blue lines in Figure 3). These results suggest that the surround facilitation is not caused by attention (see General Discussion).

General discussion

It is not completely understood how sensory stimulation that is available for a short time can be accurately perceived. For motion, previous studies indicate that in noisy conditions with weak signals, the visual system slowly accumulates sensory evidence. Here, we report that fast perception for noisy motion is possible when a surround is presented in synchrony with the motion suggesting that surrounds might be important for fast perception of motion.

Measurement of motion sensitivity from detection of coherent motion in a display of dynamic random-dots is widely used in vision science to study decision making (Gold & Shadlen, 2007; Kiani et al., 2008; Selen et al., 2012), motion integration (Britten et al., 1992; Downing & Movshon, 1989; Morrone, Burr & Vaina, 1995; Newsome & Paré, 1988; Williams & Sekuler, 1984), attentional modulation (Cook & Maunsell, 2002; Liu, Fuller & Carrasco, 2006), perceptual learning (Seitz & Watanabe, 2003) and multisensory integration (Meyer & Wuerger, 2001). The standard view is that performance on this task depends primarily on the signal-to-noise ratio (Barlow & Tripathy, 1997; Downing & Movshon, 1989; Williams & Sekuler, 1984). Here we show, however, that a task-irrelevant surround presented in synchrony with the random-dots enhances motion sensitivity. To our knowledge, this is the first report of surround facilitation to detect coherent motion.

Improvements in visual sensitivity by task-irrelevant cues transiently presented have been shown in the exogenous attention literature (Carrasco, 2011). It is unlikely, however, that the transient surround that we used was acting as an attentional cue. First, our display had no spatial uncertainty to be resolved by an exogenous cue (Ling, Liu & Carrasco, 2009; Liu, Fuller & Carrasco, 2006). Second, exogenous attentional cues enhance sensitivity when presented before the target

(Nakayama & Mackeben, 1989). In contrast, we found motion enhancement only for synchronous presentation of the surround (Experiment 5). Third, sensitivity was not enhanced when we used a single dot — a standard exogenous attentional cue (Experiment 5; Liu, Fuller & Carrasco, 2006) — regardless of the presentation timing relative to the motion target. Fourth, attentional theories do not predict the interaction that we found between the orientation of the random-lines displayed in the surround and the direction of motion of the target (Experiment 4).

Our findings suggest that transient signals are important in the facilitation of motion by a surround, which might be functionally related to the rapid analysis of scenes. Other studies, however, indicate that the sustained signal of a surround can also facilitate motion sensitivity. For example, the motion aftereffect is enhanced by the presence of a static structured surround presented for durations much longer than those for which we found the sensitivity enhancement (Day & Strelow, 1971). Also, the minimum displacement or speed necessary to detect the movement of an object is reduced when the surround contains spatial references (Aubert, 1886; Johnson & Scobey, 1982; Legge & Campbell, 1981; Leibowitz, 1955; Tyler & Torres, 1972; Whitaker & MacVeigh, 1990) — an effect that occurs even for long duration stimuli (Johnson & Scobey, 1982; Leibowitz, 1955; Tyler & Torres, 1972; Whitaker & MacVeigh, 1990). For brief stimuli, it is possible that part of the sensitivity enhancement measured using minimum motion techniques (Johnson & Scobey, 1982; Legge & Campbell, 1981; Whitaker & MacVeigh, 1990) is related to the boost by synchrony reported here, but a systematic comparison between synchronous and sustained references has not been conducted.

The spatial arrangement of our main stimulus, together with the stimulus pattern specificity shown by follow-up experiments, lead us to speculate that the facilitation might be related to the processing of relative motion by direction-selective neurons with center-surround structure (Allman et al., 1985; Loomis & Nakayama, 1973;). Many studies (Allman et al., 1985; Born & Tootell, 1992; Bradley & Andersen, 1998; Eifuku & Wurtz, 1998; Huang et al., 2007; Huang et al., 2008; Hunter & Born, 2011; Tanaka et al., 1986) demonstrate that a surround can facilitate, or suppress, the neural response to motion displayed in the center. Eifuku and Wurtz (1998), for example, showed that a static surround increases the response of medial superior temporal cortex (MSTd) neurons to a moving stimulus presented in the center. The relation between these studies and the surround facilitation that we found is, however, still uncertain because in these studies the moving stimulus was presented for long time—a situation for which we did not find facilitation. Exceptionally, Churan et al. (2008) recently reported how middle temporal (MT) neurons respond to moving gratings of different sizes presented for short time and found that motion direction is encoded more effectively by surround-suppressed neurons than by non-suppressed neurons, which they propose as a neural correlate of the behavioral surround suppression for brief stimuli (Tadin et al., 2003; Tadin et al., 2006). Whether a single mechanism with center-surround antagonistic structure (Born & Bradley, 2005; Loomis & Nakayama, 1973) can explain this behavioral suppression and the behavioral facilitation reported here might be tested in the future.

It is not self-evident, however, how a transient surround can increase the signal-to-noise ratio to improve sensitivity. If the surround facilitates or suppresses signal-dots and noise-dots in the same way, then the sensitivity based on signal-to-noise ratio would not change. One possible solution is that the surround can somehow discriminate signal-dots from noise-dots and selectively enhance the signal-dots and/or suppress the noise dots. At first, we considered this possibility because signal and noise dots had different life-times in most of our experiments (four frames for the signal-dots and one frame for the noise-dots). We later found, however, that motion was also enhanced when we matched the life-time of the signal and the noise dots (see Experiment 1), which suggests that signal and noise dots might not be segregated at the level of local motion processing. Once the motion information is pooled across dots, however, the relevant direction (left or right in our experiments) differs from the remaining directions in magnitude. It is possible that this difference is increased by surround facilitation of the relevant direction or suppression of the irrelevant ones at the stage of global pooling across directions.

We also consider three alternative mechanisms that do not necessarily require center-surround interactions. The brief presentation of a static isotropic pattern, like the synchronous surround in our experiments, generates motion energy balanced in all directions. One possibility is that this uniform distribution of motion produced by the synchronous surround serves as a comparator for the biased distribution of motion in the center. The comparator could improve the detection of coherent motion if the degree of response fluctuation by the internal noise in the uniform distribution is used to set the optimal criterion for the signal to be discriminated from the noise in the center. The comparison would not be effective for a sustained surround because it does not generate motion signal. This hypothesis, however, cannot explain why the transient surround does not facilitate coherent motion detection when it was not synchronous. The second possibility is that the similarity of the motion energy distribution produced by the synchronous surround and the noise in the center leads to perceptual grouping of the surround and the noise in the center. Then, the sensitivity could be enhanced if the grouping weakens the noise masking effect by a mechanism similar to the reduction of crowding by flanker-flanker grouping in spatial vision (Livne & Sagi, 2007). A limitation of this hypothesis is that it might be difficult to segment signal-dots from noise dots at the stage of local motion processing. The third possibility is that the motion of the surround is pooled across space and added to the motion in the center. A constant increment of motion energy for each direction could improve sensitivity if the response for each direction channel is increased with an accelerating non-linearity. A similar mechanism has been proposed to explain the dipper in the thresholds versus contrast functions (Nachmias & Kocher, 1970). This explanation suggests that the task-irrelevant transient stimulus could increase sensitivity even if it is not presented in the surround, which is not consistent with the lack of improvement by the addition of static dots to the center that we reported in Experiment 3. It awaits further investigation whether the large enhancement of motion sensitivity that we reported here is produced by the center-surround mechanism at the stage of global motion processing, one of three alternatives described in this paragraph, or something else.

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