Whether dots moving in two directions appear coherent or transparent depends on directional biases induced by surrounding motion

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When two random-dot patterns moving in different directions are superimposed, motion appears coherent or transparent depending on the directional difference. In addition, when a pattern is surrounded by another pattern that is moving, the perceived motion of the central stimulus is biased away from the direction of the surrounding motion. That phenomenon is known as induced motion. How is the perception of motion coherence and transparency modulated by surrounding motion? It was found that two random-dot horizontal motions surrounded by another stimulus in downward motion appeared to move in two oblique directions: left-up and right-up. Consequently, when motion transparency occurs, each of the two motions interacts independently with the induced motion direction. Furthermore, for a central stimulus consisting of two physical motions in left-up and right-up directions, the presence of the surrounding stimulus in a vertical motion modulated the perceptual solution of motion coherence/transparency such that if interactions with an induced motion signal narrow the apparent directional difference between the two central motions, then motion coherence is preferred over motion transparency. Therefore, whether a moving stimulus is perceived as coherent or transparent is determined based on the internal representation of motion directions, which can be altered by spatial interactions between adjacent regions.

Keywords: motion coherence, motion transparency, induced motion, motion integration

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Introduction

Motion coherence and motion transparency

The visual system integrates local motion signals across space to achieve coherent motion perception. Williams and Sekuler (1984) examined the nature and extent of integration of local motion signals across space using a random-dot kinematogram in which each dot took an independent walk in direction over time. When the distribution of directions was sufficiently narrow, the pattern often appeared to move in the mean of individual dot directions. The result shows that the visual system pools local motion signals over space to yield a percept of coherent global motion. The idea of spatial pooling has been supported by other studies of coherent motion using stimuli of various types (Amano, Edwards, Badcock, & Nishida, 2009; Bex & Dakin, 2002; Smith, Snowden, & Milne, 1994).

It is particularly interesting that, in some cases, one simultaneously perceives two global motions in independent directions at the same location of the visual field rather than one coherent motion. In such motion transparency, two overlapping surfaces appear to move over each other. For example, a random-dot pattern in which half of the dots are moving leftward and the remaining dots are moving rightward appears as two surfaces sliding horizontally over one another, not a simple averaging of two motion signals, which should be zero velocity. What kind of processing is involved in motion transparency? Qian, Andersen, and Adelson (1994) demonstrated that when a display has finely balanced opposing motion signals in all local regions, it appears as nontransparent and that the displays that appear transparent invariably contain locally unbalanced motion signals, suggesting that a processing

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stage at which local motion information is spatially pooled mediates motion transparency.

That we see motion transparency poses a difficult problem for modeling of global motion processing mechanisms (for a review, see Snowden & Verstraten, 1999). It is not known how to represent two-valued velocity information at a single location in the visual field. In addition, a phenomenological question remains as to what type of information critically determines whether stimuli should be perceived as coherent or transparent. Previous reports have described that the directional difference is one of the critical factors (e.g., Smith, Curran, & Braddick, 1999; van Doorn & Koenderink, 1982). When the angular difference between two motion directions is sufficiently large, stimuli appear as two transparent motions, but when the difference is small, one coherent motion is perceived in the averaged direction. Although arguments have been advanced as to what type of information is critical in the representation of motion direction (e.g., Jasinschi, Rosenfeld, & Sumi, 1992; Smith et al., 1999; Treue, Hol, & Rauber, 2000), these findings suggest that the information of motion direction is an important factor in the determination of whether the spatially pooled local motion signals appear as coherent or transparent.

Several reports have described a limit on the number of motion-transparent surfaces that can be perceived simultaneously. When only directional information characterizes component dots, no more than two surfaces are seen simultaneously (Edwards & Greenwood, 2005; Mulligan, 1992), although three directions are identifiable when other cues, such as speed and binocular disparity, are also provided (Greenwood & Edwards, 2006a, 2006b).

Induced motion

Motion perception is well known to be modulated by surrounding information as well. The perceived speed of a moving stimulus is affected by another motion in the vicinity or surrounding area (Loomis & Nakayama, 1973; Tynan & Sekuler, 1975; van der Smagt, Verstraten, & Paffen, 2010; Walker & Powell, 1974). More strikingly, a physically stationary stimulus appears to move in the direction opposite to that of the motion in its surround (Duncker, 1929; see Reinhardt-Rutland, 1988 for a review). The latter case is called induced motion. Such illusory motion necessarily involves multiple processing schemes including object-relative and subject-relative coordinate transformations and other global computations. In one of the most mechanistic schemes, the phenomenon is deemed to reflect local visual processing that extracts differential information, or contrast, between motion components in the close vicinity.

Previous reports have described that the perception of motion direction is modulated when induced motion occurs (Gogel, 1979; Kim & Wilson, 1997; Takemura & Murakami, 2010a). For example, a stimulus that is physically moving in a horizontal direction appears to move in an oblique direction when a surrounding stimulus moves in a vertical direction, as if a vertical induced motion were added to the physical horizontal motion. In other words, the perceived direction of the central stimulus is biased to the direction opposite to that of the motion in the surround. Consequently, in the presence of surrounding motion, the representation of motion direction is somehow modulated in a way that is consistent with the direction of induced motion as a biasing factor.

Purpose of this study

All of these phenomena (motion coherence, motion transparency, and induced motion) are extremely important for understanding how the visual system extracts object motions in a noisy environment. As reviewed above, the relation between motion coherence and transparency and the relation between central and surrounding motions have been investigated extensively. However, it has been little understood how motion coherence/transparency and induced motion are mutually related. The relation between underlying mechanisms of these phenomena also remains unclear. The outstanding questions include what happens if illusory motion is induced to a central pattern that comprises multiple directions of motion, whether the perceptual solution of coherence/transparency depends on the occurrence of induced motion, and what mechanism(s) might mediate these phenomena.

To address these issues, we examined how moving random dots in a surrounding region affect the motion coherence and transparency perceived in a central region occupied by random dots moving in two directions. As described above, the perceived direction of a moving stimulus is known to be strongly modulated by a surrounding motion as if physical and induced motions interacted. It is also known that the motion coherence and transparency depend strongly on the motion directions included in the stimulus. However, two questions remain unsolved. Question one is whether the surrounding motion biases the perceived motion directions in the center. Experiment 1 presented the answer to this question—yes. Question two is whether the way the surrounding motion biases the perceived motion directions in the center changes the way the central stimulus appears, namely, motion coherence or motion transparency. Experiments 2 and 3 addressed this question. Motion coherence/transparency and induced motion would be independent and mediated by two clearly distinct mechanisms if the answer was no. In contrast, if the answer was yes, motion coherence/

transparency and induced motion would be mediated by two mutually communicating mechanisms or even by a common processing package.

Methods

In Experiment 1, we examined how the vertical motion (up or down) in the surround modulated the perceived directions of two superimposed horizontal motions presented in the center. In Experiment 2, we presented two random-dot motions with moderate directional differences (e.g., ±45 deg from upward) in the center and a vertical motion (up or down) in the surround and examined how the surrounding motion affected the perceived direction(s) and the perception of motion coherence/transparency in the center. In Experiment 3, we randomized the physical direction of central and surrounding stimuli to examine whether the observed effect in Experiment 2 was affected by perceptual or response bias toward certain directions.

Subjects

This study, which followed Declaration of Helsinki guidelines, was approved by the Ethics Committee of the College of Arts and Sciences, The University of Tokyo. The first author (HT) and 15 subjects who were naive to the purpose of the experiment participated (aged 19–25). Each subject gave written informed consent and passed a battery of tests for visual acuity, astigmatism, and stereopsis.

Equipment

The stimulus was presented in a dark room on a 22-inch CRT monitor (RDF223H, 1280 × 960 pixels, 0.022 deg/pixel, refresh rate of 75 Hz; mean luminance of 35.74 cd/m^2; Mitsubishi Electric) controlled by a computer (PowerMac G5; Apple Computer). The viewing distance of 80 cm was maintained using a chin rest. Subjects viewed all stimuli binocularly. A programming environment (MATLAB v7.3; The Mathworks) and the Psychophysics Toolbox (Brainard, 1997) were used to generate all stimuli.

Stimuli

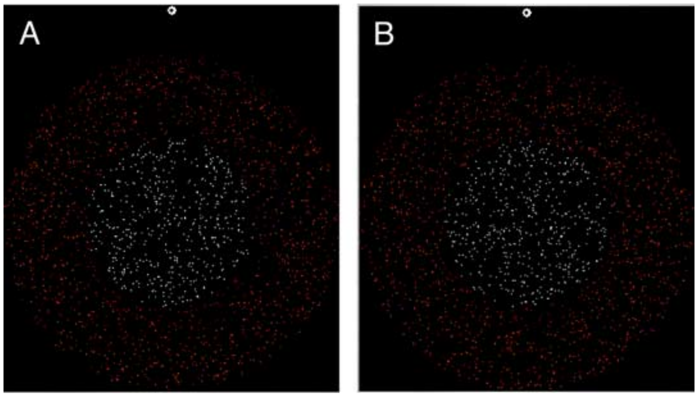
We presented two random-dot displays on a dark uniform background (0.15 cd/m^2). One random-dot display, confined within a circular static window (diameter = 3.55 deg), was called the "central stimulus." The other, which was confined within an annular static window (outer diameter = 7.1 deg) concentrically surrounding the central stimulus, was called the "surround stimulus." The central and surround stimuli, respectively, included white (77.04 cd/m^2) and red (15.7 cd/m^2) dots. The color difference was introduced merely to aid perceptual segregation between the center and surround, as used in Murakami and Shimojo's (1996) study. Dot size was 0.022 deg (1 pixel). A fixation point was provided 4.5 deg above the stimulus center. These particular values of stimulus size and eccentricity were chosen to elicit sufficiently strong induced motion and sufficiently strong motion transparency at the same time (Mestre, Masson, & Stone, 2001; Murakami, 1999; Murakami & Shimojo, 1993, 1996). The dot density was 25 dots/deg^2 for the central stimulus and 50 dots/deg^2 for the surrounding stimulus. The dot lifetime was 67–107 ms (randomly chosen from the range of 5–8 display frames). When each dot came to the end of its lifetime, it was repositioned at a randomly chosen location.

Procedure

Each trial began with the presentation of the fixation point for 2000–2500 ms. The center and surround stimuli were presented simultaneously for 507 ms (rectangular temporal window). Each was then masked immediately using a new static random noise for 507 ms. Each pixel of the static random noise had one of two luminance values—black or white—with a probability of 50% for each.

After the presentation of stimuli, subjects were asked to answer how many motions were perceived simultaneously in the center by button press. Subjects were provided with buttons of three types: Button "1" was for the percept of one coherent motion, Button "2" was for the percept of two transparent motions, and Button "3" was used for canceling the trial when the perception of the central motion was uncertain or unstable. After the button press, subjects were asked to match the perceived motion direction(s) of the central stimulus with a blue arrow-shaped visual icon (0.07 deg wide and 1.78 deg long) on the screen by rotating it about the center of the motion stimulus with a mouse cursor (direction matching paradigm, Braddick, Wishart, & Curran, 2002; Takemura & Murakami, 2010a, 2010b). The initial direction of the icon was random. During judgment, no other stimulus was presented (including the fixation point). In trials in which subjects pressed Button "2," they were asked to perform direction matching twice to answer two motion directions. In those trials, the blue icon disappeared when subjects pressed a button to finish matching the icon's direction to one of the perceived directions, immediately replaced by another red icon in a random direction. Subjects were asked to match its direction to the other perceived direction.

The direction and speed (see explanations of methods of each experiment for details) of the central stimulus were randomized within each experimental session. After each



Movie 1. Stimulus in Experiment 1. The central stimulus comprised white dots. The surround stimulus comprised red dots. (a) "Bidirectional Surround" condition. Half of the surround dots were moving upward; the other half were moving downward. (b) "Unidirectional Surround" condition. All surround dots were moving downward (or upward). All the dots (both center and surround) were moving at the same speed, namely, 1.78 deg/s when 1 pixel = 0.022 deg, as in our experimental setup.

session, subjects took a break outside the dark room. Each session comprising 24–36 trials lasted 5 min on average. Before data acquisition, all subjects experienced at least one practice session under each condition.

Experiment 1

The first author (HT) and seven naive subjects participated. The central stimulus consisted of two populations of random dots; half of the dots moved leftward and the remaining half of the dots moved rightward. We confirmed that without the surround stimulus, this display yielded vivid motion transparency perception of two random-dot patterns sliding in mutually opposite directions. Two conditions existed for the surround stimulus (Movie 1; Figure 1). In the "Unidirectional Surround" condition, a vertically moving random-dot pattern was presented within a surrounding annulus. Under this condition, the motion direction of the surround stimulus (upward or downward) was alternated between successive trials to avoid buildup of the motion aftereffect. In the "Bidirectional Surround" condition, half of the dots moved upward and the remaining half of the dots moved downward. The reason for introducing a control condition of this type was that the mere presence of temporal frequency components in the surround stimulus might reduce the visibility of the central stimulus (Takemura & Murakami, 2010a; Takeuchi & De Valois, 2000). Under the "Bidirectional Surround" condition, the temporal frequency components of the surround stimulus were identical to those under the "Unidirectional Surround" condition because the only difference between conditions was in their respective directions of motion. In addition, removing surround stimuli is not optimal control in the present study because the motion detection and discrimination performances can be modulated by the mere presence of any stimulus at adjacent locations (referenced motion; Legge & Campbell, 1981; Murakami, 2004; Shioiri, Ito, Sakurai, & Yaguchi, 2002; Tyler & Torres, 1972).

In both "Unidirectional Surround" and "Bidirectional Surround" conditions, each dot moved at 1.78 deg/s in both the central and surround stimuli. In the preliminary observation, we confirmed that this speed was sufficiently fast to cause the perceived direction shift of the central motion by presenting one horizontal motion in the center and one vertical motion in the surround. This effect did not strongly change when we used faster surrounding motion speeds (3.56 and 5.34 deg/s), suggesting that this speed was within an optimal range for eliciting an induced motion in the stimulus configuration we used.

Experiment 2

The central stimulus consisted of two populations of dots moving in the symmetrical directions about the vertical axis: ±15, ±19, ±27, and ±45 deg deviating from the upward or downward direction. Hereinafter, we label these directional differences, respectively, as "30°," "38°," "54°," and "90°." We tested two different speed conditions. In the "Slower" speed condition, the speed of dots were, respectively, 6.71, 5.15, 3.64, and 2.3 deg/s for the directional differences of "30°," "38°," "54°," and "90°." In the "Faster" speed condition, the respective speeds were 13.42, 10.3, 7.28, and 4.63 deg/s. In both "Slower" and "Faster" speed conditions, the speed component in the horizontal direction was identical across different directional differences. For two reasons, we matched horizontal speeds. First, we sought to avoid using subpixel animation whenever possible. In the current stimulus presentation protocol, all dot positions had integer values on x–y pixel coordinates on the monitor. For example, in the "Slower" speed condition, dots moved by just 1 pixel per frame in the horizontal direction and moved by 1, 2, 3, and 4 pixels

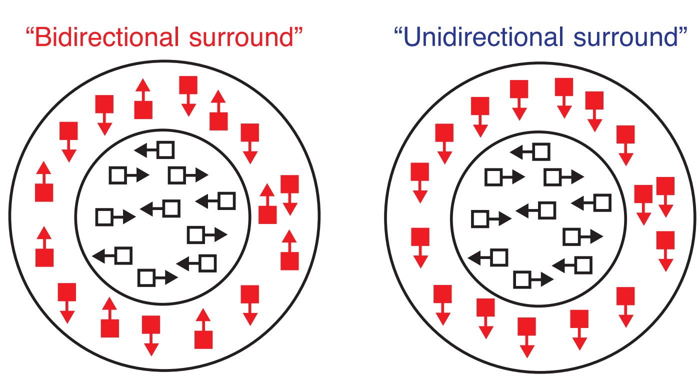
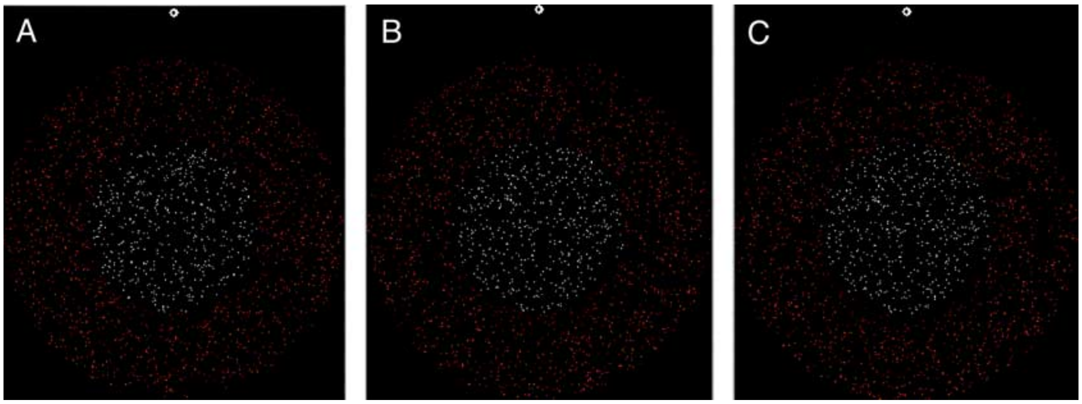


Figure 1. Schematic illustration of the stimulus used in Experiment 1.



Movie 2. Stimulus used in Experiment 2. Surround dots were moving at 1.78 deg/s. Central dots were moving at 2.3 deg/s. Central motion directions were ±45 deg from the upward direction in this particular display ("90°," "Slower" condition). (a) "Same Surround" condition. All surround dots were moving in the same direction as the average direction between the two central motions (i.e., upward). (b) "Bidirectional Surround" condition. Half of the surround dots were moving upward; the other half were moving downward. (c) "Opposite Surround" condition. All surround dots were moving in the direction opposite to the average direction between the two central motions (i.e., downward).

per frame in the vertical direction in the "90°," "54°," "38°," and "30°" conditions, respectively. Second, in preliminary observations, the central stimuli were often perceived as being stationary at small directional differences (e.g., in the "30°" and "38°" conditions) when we used slower speeds (e.g., 2.3 deg/s). To achieve robust motion perception in all conditions, we had to use faster central stimulus speeds at smaller directional differences. Although the speed of the central stimulus was varied across conditions, the speed of the surround stimulus remained constant (1.78 deg/s).

Three conditions were identified for the surround stimulus. The "Bidirectional Surround" condition was identical to that in Experiment 1; half of the dots moved upward. The other half moved downward. In the "Same Surround" condition, all surround dots moved in the mean direction of the two central motions. In the "Opposite Surround" condition, all surround dots moved in the direction opposite to the mean direction of the two central motions. Movie 2 and Figure 2 present examples of the "Same Surround," "Bidirectional Surround," and "Opposite Surround" conditions.

Eight subjects participated under all conditions. For the remaining eight subjects, only "54°" and "90°" directional differences in the "Slower" speed condition were tested. The three surround stimulus conditions were tested in random order across sessions. Under the "Same Surround" and "Opposite Surround" conditions, the overall motion direction of the display (upward or downward) was alternated between trials to avoid buildup of the motion aftereffect.

Experiment 3

In Experiment 3, we examined the replicability of Experiment 2 when the motion direction of the stimulus as a whole was not fixed along the vertical axis but was

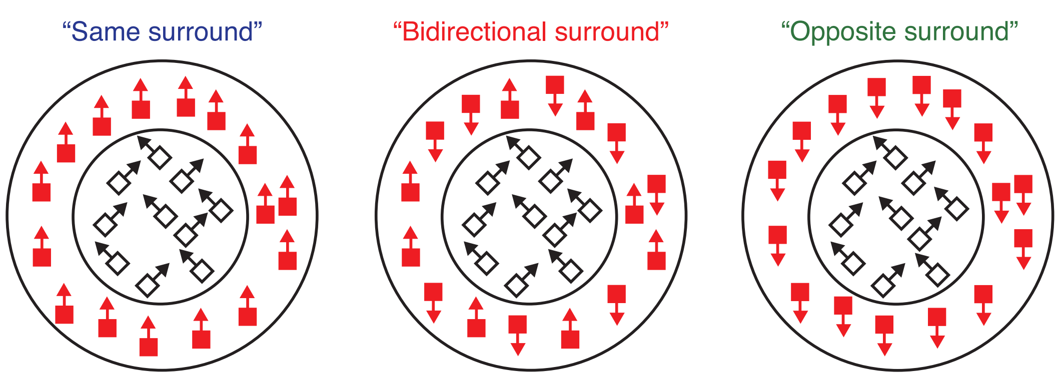


Figure 2. Schematic illustration of the stimulus used in Experiment 2.

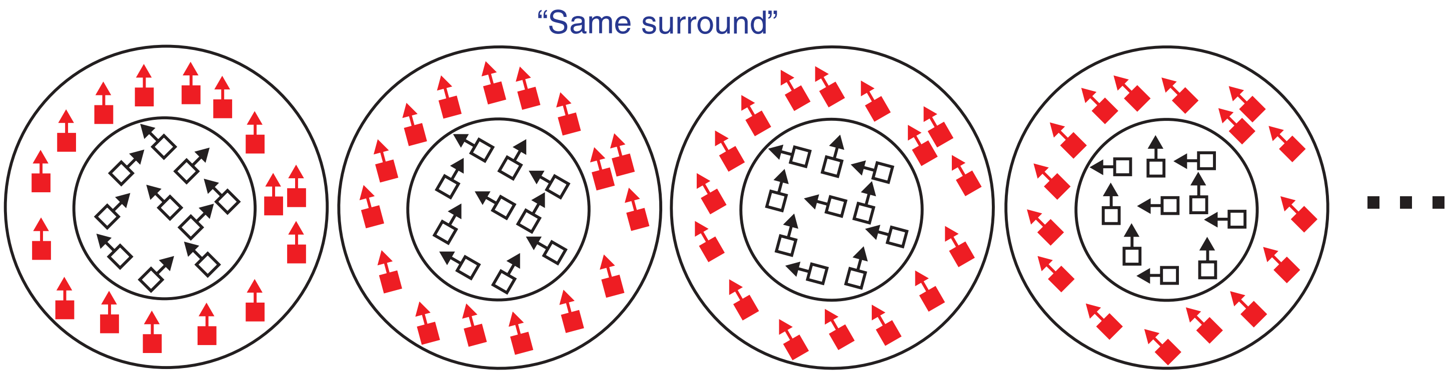


Figure 3. Schematic illustration of the stimulus used in Experiment 3 (examples from the “Same Surround” condition). The overall direction of the stimulus that determined the motion directions of the central stimuli was chosen randomly for each trial, whereas the directional relation between the central and surround stimuli was maintained (in the case shown here, the surround dots moved in the average direction of the central two motion components).

instead randomized to exclude perceptual or response bias toward certain directions. The first author (HT) and three subjects participated. Only the “90°” directional difference in the “Slower” speed condition in Experiment 2 was tested again in this experiment. The overall direction of motion was no longer restricted within the vertical direction but was instead randomly chosen from 0, 15, 30, …, 345 deg, whereas the relation of motion directions between center and surround stimuli was kept constant. Consequently, in each trial, we presented a randomly rotated version of either one of the stimuli shown in Figure 2. Some schematic examples are portrayed in Figure 3. Dot positions were calculated at subpixel accuracy and rounded to the nearest pixel position.

Results

Experiment 1: 180-deg directional difference

In this experiment, half of the dots moved leftward; the remaining half of the dots moved rightward. Subjects reported the percept of “two transparent motions” in most trials in both conditions (94.5% under the “Unidirectional Surround” condition and 95.0% under the “Bidirectional Surround” condition). The “one coherent motion” percept was reported in only a few trials (2.4% under the “Unidirectional Surround” condition and 4.4% under the “Bidirectional Surround” condition). The canceling button was pressed very rarely (3.1% under the “Unidirectional Surround” condition and 0.1% under the “Bidirectional Surround” conditions). Therefore, this report describes the results of direction matching in the trials when the subjects reported the percept of “two transparent motions” (Figure 4). The results were formatted as radar charts. For the “Bidirectional Surround” condition, 0 deg denotes upward. For the “Unidirectional Surround” condition, 0 deg denotes the direction opposite to that of the surround stimulus. Consequently, all responses were shown as if the surround stimulus was moving downward.

Under the “Bidirectional Surround” condition, subjects very frequently reported a pair of horizontal motions. The

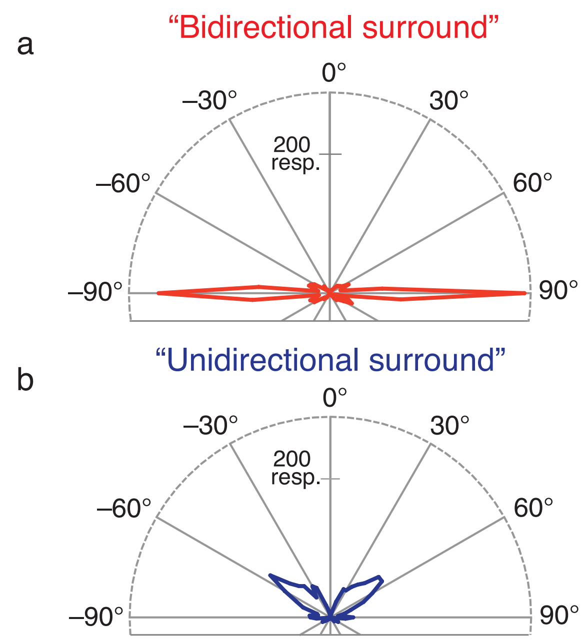


Figure 4. Results of Experiment 1. Histograms show the number of trials for the perceived direction of the test stimulus in the (a) “Bidirectional Surround” condition and (b) “Unidirectional Surround” condition: “0” denotes exactly vertical, and “90” denotes exactly horizontal movement. Only results of trials in which subjects reported “two transparent motions” (by pressing Button “2”) are included. Under the “Unidirectional Surround” condition, this format was used to show the perceived direction of the test stimulus when it was physically moving horizontally (rightward and leftward) and the adapting stimulus was physically moving downward. Data obtained under the mirror-symmetrical condition in which the adapting stimulus was physically moving upward were reversed and merged.

reported pairs of directions were within ±20 deg around exactly horizontal directions (+90 and −90 deg) in 61.0% of all trials. Therefore, that perception was mostly veridical because the central stimulus indeed included leftward and rightward motions. In contrast, under the "Unidirectional Surround" condition, subjects reported two oblique directions in most trials. These directions were clearly biased away from the motion direction of the surround stimulus by approximately 40 deg. This deviation from the horizontal was significant (two-tailed Z-test, $p < 0.001$ for both the rightward response data and the leftward response data). Under both conditions, it was also confirmed that two virtually symmetrical motion directions about the vertical axis were always reported within each single trial. The correlation between the two directional responses was significant ($r = -0.91$, $p < 0.001$).

As we remarked above, subjects reported "one coherent motion" in a low percentage of trials (2.4% under the "Unidirectional Surround" condition and 4.4% under the "Bidirectional Surround" condition). The perceived directions in these trials are worth mentioning. In the "Unidirectional Surround" condition, subjects reported an exactly vertical direction (median: ±1.7 deg from the vertical), which probably occurred because the repulsive effect away from the surround motion was so strong in these trials that the directional difference between the two central motions became negligible in the visual system, and as a result, they were perceptually integrated into one vertical coherent motion. We further examined this issue in Experiment 2. In the "Bidirectional Surround" condition, subjects reported an exactly horizontal direction (median: ±90 deg from the vertical). We consider that this is simply because subjects attentively focused on only one of the two opposite directions, missing the other one. Although we proceed with no further analysis of such trials because their number is small, these data are consistent with the observed effects in the trials in which subjects reported two transparent motions (Figure 4).

These results indicate that the surrounding motion simultaneously modulates the perceived direction(s) of the two central motions. The surrounding motion is well known to modulate the perceived direction of a single motion such that it appears as if it is moving away from the surround or in a direction that is predicted from a vector sum between the actual direction of the central motion and an induced motion signal (Gogel, 1979; Kim & Wilson, 1997; Takemura & Murakami, 2010a). In the present experiment, such perceptual interactions with an induced motion signal were shown to occur simultaneously in each of the two motion-transparent patterns.

In contrast, the surround stimulus did not modulate the perceived directions under the "Bidirectional Surround" condition, in which downward and upward motions coexisted in the surround stimulus, yielding a situation of motion transparency in the surround stimulus itself. Previously, Murakami (1999) investigated whether induced motion occurred for a static stimulus when two independently moving dot patterns surrounded it. Subjects reported induced motion in the direction opposite to the averaged direction of the two surrounding inducers. This previous study suggested that when the surrounding motion includes multiple directions, its perceptual influence on the central static stimulus acted in a vector-summation manner. Based on this finding, we argue that under the "Bidirectional Surround" condition of the present experiment, the induced effects of two opposing motions might be canceled out, engendering a lack of overall influence on the central stimulus.

Experiment 2: Less than 180-deg directional difference

In this experiment, the central stimulus moved in oblique directions. Subjects pressed the canceling button in a few trials. Table 1 presents the percentage of the aborted trials under each condition for eight subjects who completed all conditions. We subtracted the quantities of aborted trials before calculating the relative frequencies of particular percepts explained in the following.

Figure 5 presents the probability of seeing "two transparent motions" under each condition for eight subjects. In several cases, subjects reported the percept of "two transparent motions" more frequently under the "Same Surround" condition than under the "Bidirectional Surround" condition. This difference in relative frequency was statistically significant for the directional differences of "38°," "54°," and "90°" under the "Slower" speed condition (two-tailed Z-test with Bonferroni correction: $p < 0.001$) and for the directional difference of "38°" under the "Faster" speed condition (two-tailed Z-test with Bonferroni correction: $p < 0.05$). In addition, subjects reported the percept of "one coherent motion" more frequently under the "Opposite Surround" condition than under the percept under the "Bidirectional Surround" condition or for the directional difference of "90°" under the "Slower" speed condition (two-tailed Z-test with Bonferroni correction: $p < 0.001$). When we compared

	"90°"	"54°"	"38°"	"30°"
(a) "Slower" condition				
"Opposite Surround"	1.8%	1.3%	1.1%	0.8%
"Bidirectional Surround"	3.6%	0.9%	0.8%	0.9%
"Same Surround"	10.5%	6.4%	1.5%	0.9%
(b) "Faster" condition				
"Opposite Surround"	0.8%	1.0%	0.4%	0.4%
"Bidirectional Surround"	1.0%	1.3%	1.1%	0.8%
"Same Surround"	1.1%	1.0%	0.8%	0.4%

Table 1. Percentage of aborted trials in Experiment 2: (a) data under the "Slower" speed condition and (b) data under the "Faster" speed condition.

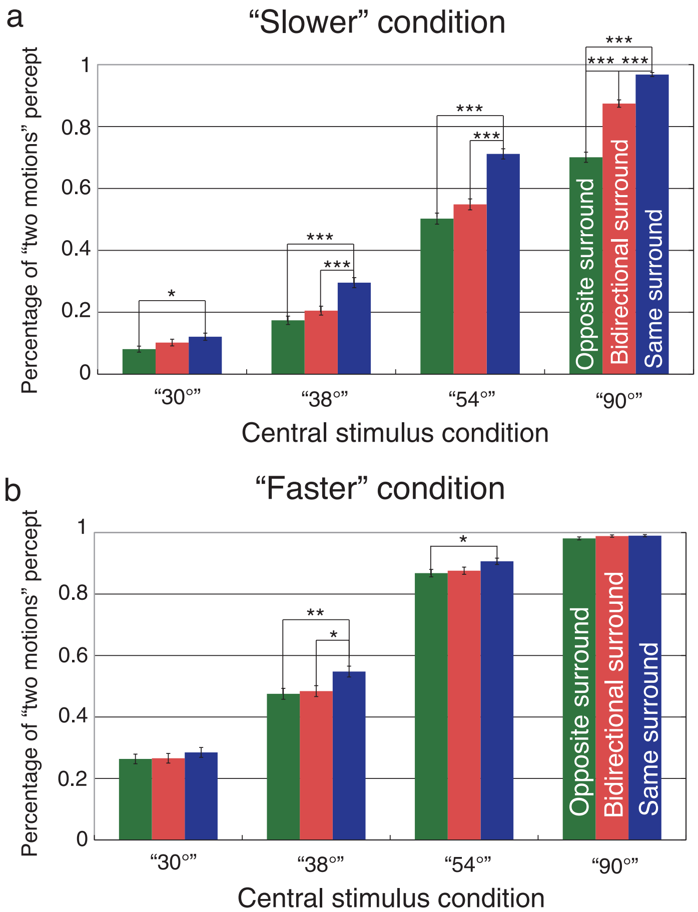


Figure 5. Percentage of reporting “two transparent motions” in Experiment 2 (N = 8): (a) data under the “Slower” speed condition and (b) data under the “Faster” speed condition. The abscissa shows the central stimulus conditions. Bars of different colors represent data under different surround stimulus conditions (blue, “Same Surround”; red, “Bidirectional Surround”; green, “Opposite Surround”). Trials in which subjects pressed the canceling button were excluded from analyses. Error bars represent ±1 *SEM*. Asterisks denote significant differences (two-tailed Z-test with Bonferroni correction: *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$).

the “Same Surround” and “Opposite Surround” conditions in the same statistical criterion, a significant difference was confirmed for “38°,” “54°,” and “90°” under the “Slower” speed condition (two-tailed Z-test with Bonferroni correction: $p < 0.001$), “30°” under the “Slower” speed condition (two-tailed Z-test with Bonferroni correction: $p < 0.05$), “54°” under “Faster” speed condition (two-tailed Z-test with Bonferroni correction: $p < 0.05$), and “38°” under “Faster” speed condition (two-tailed Z-test with Bonferroni correction: $p < 0.01$). These results show that the surrounding motion modulates the perception of motion coherence and transparency of the central motion signals.

Insufficient evidence for such modulations under the “Faster” speed condition suggests that the effects of the surround have speed specificity to some degree, manifesting themselves only when the central stimulus was moving at sufficiently slow speeds, thereby presumably being more susceptible to motion induction from the surround. This consideration is also consistent with the general lack of significant differences at smaller directional differences, such as “30°,” even under the “Slower” speed condition, because our central stimulus became faster with decreasing directional differences (see Methods section). Results also showed that the central motions were categorized more frequently as “two transparent motions” under the “Faster” speed condition than under the “Slower” condition. Moreover, this difference was statistically significant for all surround stimulus conditions and directional differences (two-tailed Z-test: $p < 0.001$).

To provide a more comprehensive view of what directional alteration was induced to the central motions by the surround stimulus, we present results of direction matching under the “Slower” speed condition and “90°” directional difference condition, as a relative frequency of the perceived direction in the format of a radar chart (Figure 6). Separately, we show the direction matching results depending on whether “one coherent motion” was reported by pressing Button “1” or whether “two transparent motions” were reported by pressing Button “2.” Data obtained for the physical motion directions of $\pm x$ deg around the downward direction were flipped and merged to data obtained for those of $\pm x$ deg around the upward direction. Consequently, the data should appear as if the central stimulus always contained two motions in $\pm x$ deg directions around the upward direction (0 deg).

Under the “Bidirectional Surround” condition, “two transparent motions” were reported in most trials (87.7%). In this case, the perceived directions of the central stimulus reported by direction matching (median: ±56.7 deg from the vertical) did not differ greatly from the physical motion directions (±45 deg), although they were significantly closer to the horizontal than the actual directions (two-tailed Z-test, $p < 0.001$ for both the rightward response data and the leftward response data). This deviation was expected from the well-documented phenomenon of direction repulsion that is often observed in displays containing two motions with their directional difference of around 90 deg (Curran, Clifford, & Benton, 2009; Marshak & Sekuler, 1979; Mather & Moulden, 1980; Snowden, 1989; Wilson & Kim, 1994).

However, under the “Same Surround” condition, the profile of perceived direction changed greatly: Subjects frequently reported two horizontal directions. The perceived directional difference between two motions became much greater than that in the “Bidirectional Surround” condition (two-tailed Z-test: $p < 0.001$). The reported directions (median: ±80.5 deg from the vertical) deviated significantly from 45 deg (two-tailed Z-test, $p <$ 0.001 for both the rightward response data and the

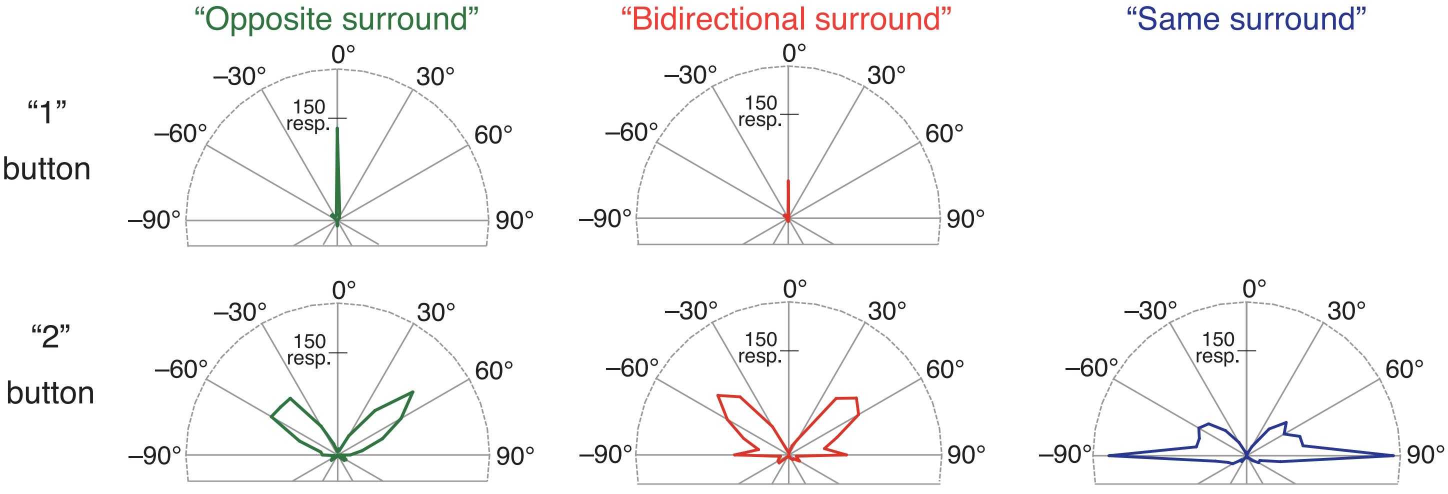


Figure 6. Direction matching results obtained under "90°" condition at the "Slower" speed (N = 8). Trials in which subjects reported "one coherent motion" and "two transparent motions" are shown separately. Other configurations are identical to those shown for Figure 4.

leftward response data). Under this condition, the radar chart was formatted as though the surround stimulus was always moving in 0 deg, the same direction as the average of the two motions in the central stimulus. The actual data indicate clearly that perceived directions were biased away from upward: They were biased toward induced motion in the downward direction induced by the upward moving surround stimulus. In addition, the overall shape of the direction histogram changed radically from that under the "Bidirectional Surround" condition to a skewed profile, peaking at ±90 deg bins. Consequently, in 41.1% of all trials, the central stimulus physically moving in ±45 deg directions was judged as moving in directions within ±20 deg around exactly horizontal directions (+90 and −90 deg).

What type of perception occurred under the "Opposite Surround" condition? Under this condition, "one coherent motion" was reported more frequently (30.8%). In these trials, subjects reported an exactly vertical direction in direction matching (Figure 6), indicating that the two motion components (±45 deg) in the central stimulus were perceptually integrated into the averaged (vertical) direction. In the remaining trials, in which subjects reported "two transparent motions," the direction histogram shows two oblique motion directions (median: ±51.9 deg from the vertical) that did not differ greatly from the physical directions (±45 deg). We consider that the perceived motion direction was modulated by surrounding motion under this condition as well. The perceived direction of a central stimulus is known to be biased away from surrounding motion (e.g., Kim & Wilson, 1997). Therefore, the directional difference between the two central motions should become perceptually smaller than the physical difference. If such an "induced" directional difference were too small to establish transparent motion percept, then these motions would be perceived as one coherent motion in the averaged direction. We address this issue again in the General discussion section.

Figure 7 portrays the direction matching results as histograms for the conditions under which a significant difference was found in the percentage of "two transparent motions" between the "Same Surround" and "Bidirectional Surround" conditions. In Figure 7, the data for trials in which subjects reported "one coherent motion" and "two transparent motions" are shown, respectively, as open and filled symbols. Overall, directions near the vertical (e.g., ±10 and ±20 deg) were rarely reported, suggesting that two motion components were perceptually integrated. They came to have exactly vertical motion when the directional difference was small. Still, Figures 7c and 7d show that when the actual directions were ±19 deg, the directions within 20–30 deg were reported in a certain fraction of all trials. Such reports occurred more often under the "Same Surround" condition, suggesting more frequent transparent motion perception by the help of an induced motion signal under this condition.

To examine the possibility that our main results presented in Figures 5 and 6 were derived simply from a sampling bias in choosing the subjects, we doubled the number of subjects for a subset of conditions for which significant differences were found, namely, the "54°" and "90°" directional differences at the "Slower" speed. Figure 8 portrays the results for such a larger population of subjects (N = 16) in "54°" and "90°" under the "Slower" speed condition. Still, results showed that subjects reported "two transparent motions" more frequently under the "Same Surround" condition (for both "54°" and "90°" directional differences), and less frequently under the "Opposite Surround" condition (only for "90°"), than under the "Bidirectional Surround" condition (Figure 8a). These

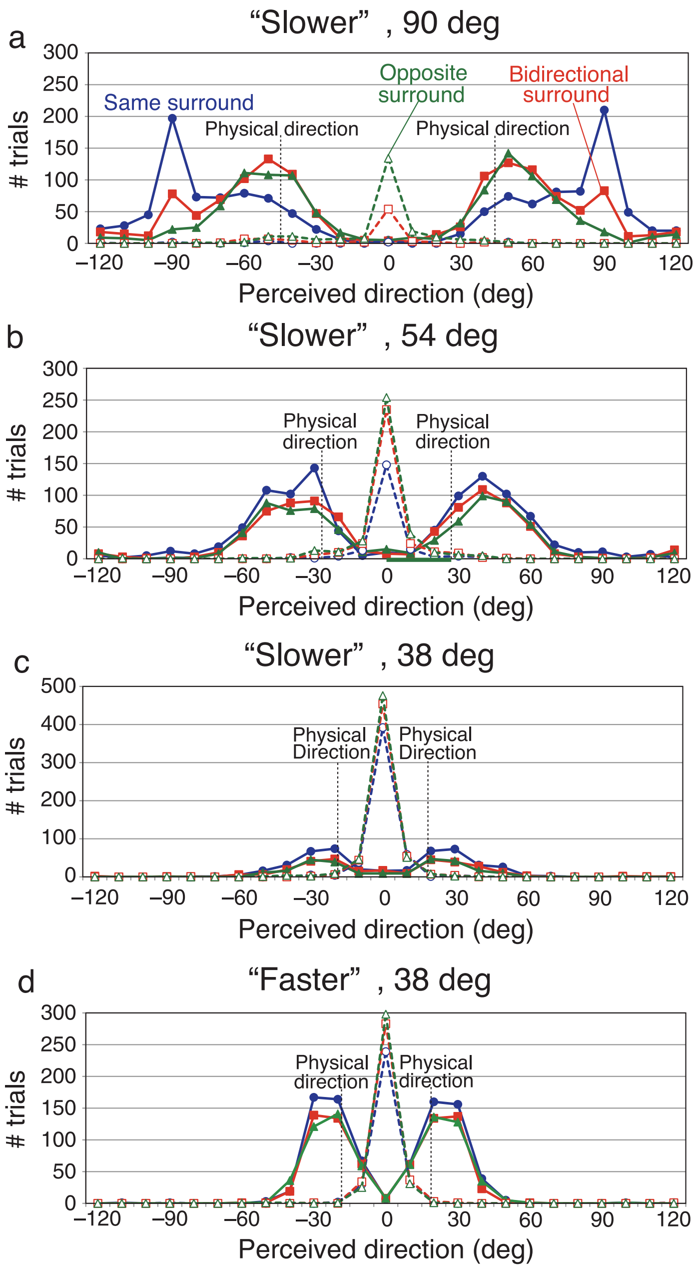


Figure 7. Histograms of direction matching results (N = 8). The horizontal axis shows the perceived direction of central motions ("0" denotes vertical, positive values signify rightward directions, and negative values signify leftward directions). Trials in which subjects reported "one coherent motion" are denoted by open symbols with dotted lines. Trials in "two transparent motions" are denoted by filled symbols with solid lines. Circles, triangles, and squares, respectively, signify the data under the "Same Surround," "Opposite Surround," and "Bidirectional Surround" conditions: (a) "90°" and "Slower" speed, (b) "54°" and "Slower" speed, (c) "38°" and "Slower" speed, and (d) "38°" and "Faster" speed.

differences were statistically significant (two-tailed Z-test with Bonferroni correction: $p < 0.001$). The direction matching results (Figures 8b and 8c) was also similar to the results presented in Figures 6 and 7. The reported directions were biased toward the horizontal direction under the "Same Surround" condition.

Experiment 3: 90-deg directional difference and random overall motion direction

In this experiment, the "90°" directional difference condition at the "Slower" speed in Experiment 2 was replicated but with a randomly rotated stimulus to examine whether the observed effects in Experiment 2 depended on perceptual or response bias toward certain directions. The motion direction of the overall stimulus was randomized, although the directional difference between the central two motions was kept constant at 90 deg. The directional relation between the central and surround stimuli were also maintained (Figure 3). Figure 9 portrays the results, which were consistent with those of Experiment 2: Subjects more frequently reported "two transparent motions" under the "Same Surround" condition and more frequently reported "one coherent motion" under the "Opposite Surround" condition. Under both conditions, the percentage reporting "two transparent motions" was significantly different from that under the "Bidirectional Surround" condition (two-tailed Z-test with Bonferroni correction: $p < 0.001$). Figures 9b and 9c portray the results of directional matching. In these plots, "0°" represents the average direction of the central two motions (which was always in the vertical direction in Experiment 2 but randomly variable in Experiment 3). In trials where subjects reported "one coherent motion," they reported motion directions around "0°" in most trials, suggesting that the two motion components were perceptually integrated. This was consistent with the results obtained in Experiment 2. However, a slightly different pattern was observed in the results from trials in which subjects reported "two transparent motions." First, the histograms became rounder than those in Experiment 2, indicating greater noise in the data. We interpret this as an unavoidable trend because the task of directional matching in this experiment was much more demanding than in the case of the fixed absolute direction. Second, the perceived directions under the "Same Surround" condition were still biased away from the direction of surround motion as compared with those under other conditions. A significant difference in perceived directions was found between the "Same Surround" and "Bidirectional Surround" conditions (two-tailed Z-test with Bonferroni correction: $p < 0.005$). A significant difference in perceived directions was also found between the "Bidirectional Surround" and "Opposite Surround" conditions (two-tailed Z-test with Bonferroni correction: $p < 0.001$). Third, although the perceived directions were biased away, they rarely hit just horizontal directions, unlike Experiment 2. Thereby, the reported directional differences became much smaller than those in Experiment 2 (median: ±50.1 deg from the average direction of the

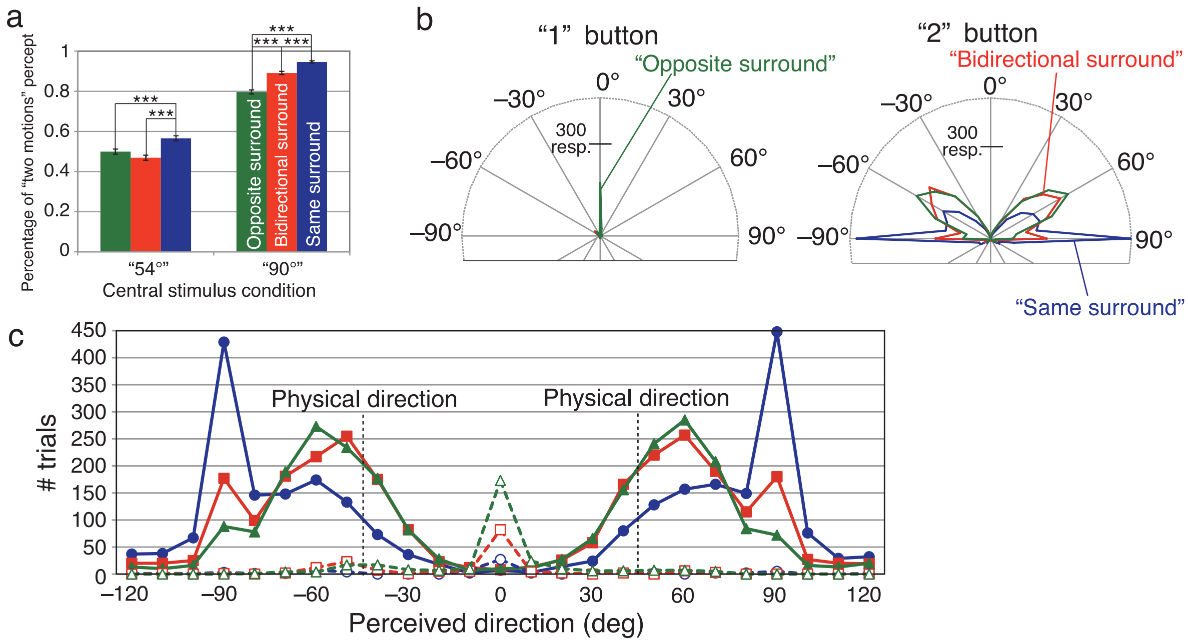


Figure 8. Results for a larger population of subjects (*N* = 16). (a) Percentage of reporting "two transparent motions." Central stimulus conditions correspond to the third and fourth ones in Figure 5a: the "54°" and "90°" directional differences at the "Slower" speed. Conventions are identical to those shown for Figure 5. (b) Direction matching results obtained under the "90°" condition. Trials in which subjects reported "one coherent motion" and "two transparent motions" are shown separately. Conventions are identical to those described for Figure 6. (c) Histogram of direction matching results obtained under the "90°" condition. Conventions are identical to those described for Figure 7.

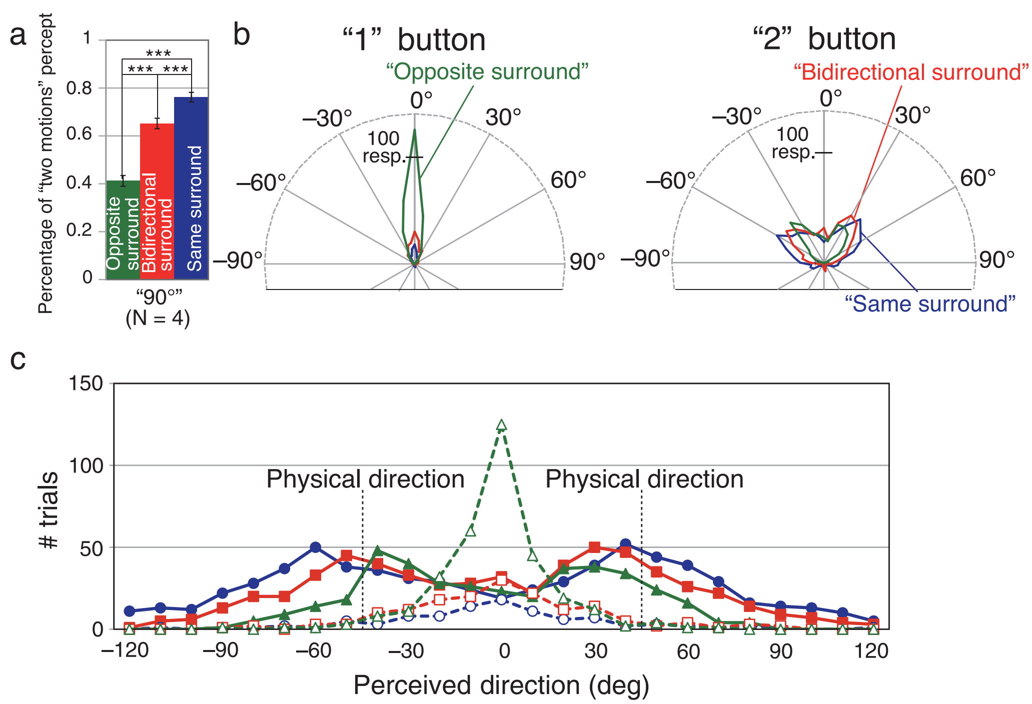


Figure 9. Results of Experiment 3 (*N* = 4). (a) Percentage of reporting "two transparent motions." Conventions are identical to those described for Figure 5. (b) Direction matching results; "0" denotes the mean direction between the central two motions (its meaning is identical to the vertical direction in Experiment 2). Other conventions are identical to those described for Figure 6. (c) Histogram of direction matching results. Conventions are identical to those of Figure 7.

central two motions). This pattern of results suggests that a perceptual or response bias toward the horizontal directions affected the results obtained for Experiment 2, in which the absolute overall direction of the stimulus was fixed at the vertical. Actually, subjects reported exactly horizontal directions very frequently in Experiment 2, especially under the "Same Surround" condition (Figures 6 and 7; "90°," "Slower" speed). These sharp peaks at the horizontal directions diminished when the overall motion direction was randomized in Experiment 3 (Figures 9b and 9c). The bias toward the horizontal directions in Experiment 2 might be explained by reference repulsion described in reports of previous studies (Jazayeri & Movshon, 2007; Stocker & Simoncelli, 2008). In Experiment 2, subjects would tend to judge perceived directions relative to the vertical direction because the averaged direction of the central motions was always exactly vertical. If such a consistent reference in the vertical direction affected the judgment, then it is possible that direction matching results showed a stronger repulsion effect in Experiment 2, in comparison with those obtained in Experiment 3. In any event, as Figure 9a shows, the modulation of motion coherence/transparency by surrounding motion was replicated even when we excluded the effect of such a horizontal bias in this experiment. These results suggest that a perceptual or response bias toward certain directions was not a critical factor for the modulation of motion coherence/transparency by surrounding motion.

In summary, these results demonstrate that the surrounding motion modulates the representation of central motion directions in two nearby directions. Central motions were integrated perceptually into a single coherent motion or segregated to two transparent motions according to the modulation of directional representation by the surrounding motion.

General discussion

Dependence of motion coherence/transparency on induced motion

This study revealed that surrounding motion modulated the perceived direction of two central motions simultaneously (Experiment 1). Additionally, results show that modulation of the perception of motion coherence and transparency by surrounding motion was accompanied by changes of perceived directions of central motions (Experiment 2). This modulation of motion coherence/transparency was observed consistently when the overall motion direction of the stimulus was determined randomly (Experiment 3).

Although previous studies demonstrated that the perception of motion coherence and transparency depend strongly on the representation of motion direction (Smith et al., 1999; Treue et al., 2000; van Doorn & Koenderink, 1982), no previous study addressed the question of whether the physical direction or the perceived direction modulated in the presence of induced motion is critical. In addition, it was unknown to what degree the underlying mechanisms of motion coherence/transparency and induced motion might be mutually independent. This study demonstrated that the perception of motion coherence and transparency depends on the perceived motion directions that are modulated by surrounding motion. The present results support the view that these motion phenomena of two kinds (motion coherence/transparency and induced motion) are mediated by two mutually communicating mechanisms or even by a common motion-based segmentation mechanism that includes differencing and integrating among motion components placed at the same and adjacent locations in the visual field.

It is difficult to elucidate whether these two phenomena are mediated by one common mechanism or two separate but strongly interacting mechanisms. One plausible interpretation is that the observed effect of surrounding motion in the present study shares a common fundamental mechanism with the phenomenon known as "direction repulsion" or overestimation of the direction difference between two transparent motions in nearby directions (Curran et al., 2009; Marshak & Sekuler, 1979; Mather & Moulden, 1980; Snowden, 1989; Wilson & Kim, 1994). Because of the similarity of the phenomena, Anstis (1986) described direction repulsion as a variant of induced motion. Direction repulsion has been explained as lateral inhibition between direction-selective motion processing units (Wilson & Kim, 1994). Because the units that are selective to the two directions mutually send inhibitory signals, the perceived directions are biased away from each other as a result of population coding. This idea is similar to local mechanistic explanations for induced motion in terms of the contrasting influence from adjacent locations via lateral inhibition across motion processing units (Kim & Wilson, 1997; Walker & Powell, 1974). In the present study, we found that the perceived directional difference between the two central motions became larger or smaller depending on the direction of the surrounding motion (Figure 6). It is possible to interpret these results as a facilitation and suppression of direction repulsion: The surrounding motion simply facilitates or suppresses the existing mutual inhibitions in direction-selective motion processing units that process motion signals at the same location in the visual field. If this interpretation is correct, then such inhibitory connections might be regarded as a common mechanism that can yield conventional unidirectional induced motion or direction repulsion of two motions depending on how many directions of motion are represented in the region surrounded by the inducer. In addition, the same inhibitory network might provide a critical representation of motion directions that determines whether an incoming stimulus should appear to move coherently or transparently. In the Model section, we present the manner in which such ideas of inhibitory connection can explain the results obtained in this study.

Effect of perceived speed

Another important issue is the relation of the present results to perceived speed. Experiment 2 revealed that central motions were categorized more frequently as "two transparent motions" when the central speed was faster, even though the directional difference was equivalent. Consequently, it is worth consideration that surrounding motion affects perceived speed, which has been reported to occur depending on stimulus configuration and luminance contrast (van der Smagt et al., 2010), and that this perceived speed subsequently affects perceived directions. We confirmed that the surrounding motion suppressed the perception of motion in the same direction as that of the surround and enhanced the perception of motion in the opposite direction in our stimulus configuration (Figure 4). Based on these findings, we predict that the perceived speed of the central stimulus should become slower under the "Same Surround" condition and faster under the "Opposite Surround" condition. Actually, under the "Same Surround" condition, and especially when the speed condition was "Slower," subjects used the canceling button in a larger number of trials (Table 1). These results support our view that the perceived speed became slower under the "Same Surround" condition. As described above, faster motions are segregated more readily in general (van Doorn & Koenderink, 1982). However, in Experiment 2, even though the perceived speed presumably became slower, subjects categorized the central stimulus as "two transparent motions" much more frequently than as "one coherent motion" under the "Same Surround" condition. Therefore, the present results cannot be explained by the modulation of speed by surrounding motion.

Subjective and objective experimental methods for the perception of motion coherence and transparency

Previous psychophysical studies have examined the perception of motion transparency using both subjective (e.g., McOwan & Johnston, 1996; Qian et al., 1994; Stoner, Albright, & Ramachandran, 1990) and objective methods (e.g., Braddick et al., 2002; Edwards & Greenwood, 2005; Masson, Mestre, & Stone, 1999). For the present study, we used a subjective method to examine the effects of surrounding motion on motion coherence/transparency because we believe that it is the optimal method in light of our research purposes. First, we can measure the observer's subjective perceptual experiences of motion transparency directly. Second, had we introduced objective methods (e.g., a 2AFC between physically coherent motion and transparent motions), subjects could have used any kind of cue (speed, trajectory, or any other noticeable difference in the distribution of motion directions and in other statistics) that appeared within the stimulus to discriminate different stimuli irrespective of whether the stimulus is perceived subjectively as transparent motion or not. Even if two central motions were perceptually integrated, it would be possible for subjects to discriminate this perceptually integrated motion from physically coherent motion using other cues. One possible solution would be to manipulate the signal-to-noise ratio of the central stimulus (e.g., Edwards & Greenwood, 2005) to match the appearance of coherent motion and transparent motions. However, this method is not useful in the present study because the magnitude of induced motion is known to change with the noise level (Hanada, 2004, 2010) and luminance contrast (Murakami & Shimojo, 1993, 1996) of the central stimulus. One disadvantage of subjective methods is that the results can be affected by individual differences in the decision criterion. We obtained data from a sufficiently large number (N = 16) of observers in the main experiment (Figure 8) to limit the effects of individual differences drastically.

Model

What model accounts for the results of the present experiments? One simple idea would be that central physical motions are integrated with the induced motion signal in a vector-sum manner that is similar to motion integration between physically superimposed motions. A model of this type can well account for the results in the "Opposite Surround" condition. In this case, the induced motion component arises in the average direction between those of the central two motions, namely, the upward direction in Figure 10. This additional component can help integrate the multiple motion components into one coherent motion (e.g., Treue et al., 2000), raising the frequency of seeing one motion, which is exactly the result obtained in Experiments 2 and 3. However, this does not work for explaining the results in the "Same Surround" condition. The induced motion component appears in the direction opposite the average between the central two motions. If these three motions coexisted, then the subject would perceive motion transparency between upward and downward motions because the directional difference between the two oblique motions is less than the difference between the induced motion and either one of the oblique motions, or the subject would perceive three transparent surfaces (e.g., Greenwood & Edwards, 2006a) or a multistable view of fewer surfaces (e.g., Jazayeri, Wallisch, & Movshon, 2010; Shooner & Movshon, 2011). No subject reported three surfaces or multistable perception in our experiment but most stably

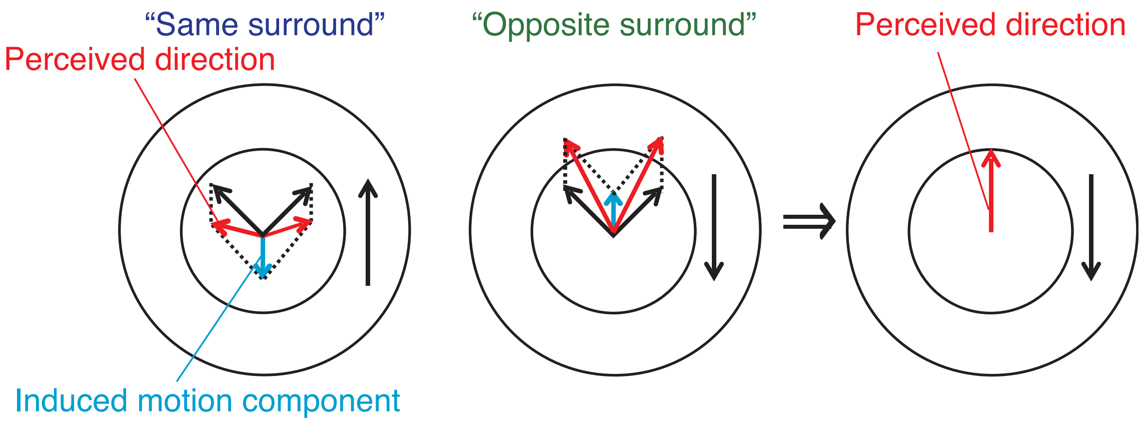


Figure 10. Model accounting for the present results, incorporating vector summation between induced motion and physical motion. Individual physical motions (black arrows) in the center are simultaneously integrated with induced motion (blue arrow). Consequently, the perceived direction of each motion component was modulated independently (red arrows).

saw two shallower-than-actual directions of motions in most trials. Consequently, simple vectorial integration cannot predict the actual results obtained under the "Same Surround" condition if we assume that the induced and physical motions are integrated in a way that is analogous to the mode of integration among physically superimposed motions.

Another modeling idea is to treat integration between induced and physical motions as a different matter than integration between physical motions. In this model, the induced motion is integrated independently (e.g., in vector-sum manner) with each of the individual physical motions in the center (Figure 10). Two shallower-than-actual motions are perceived under the "Same Surround" condition because induced motion pulls down the two oblique motions simultaneously. Under the "Opposite Surround" condition, the two oblique motions are pulled up simultaneously to steeper-than-actual directions. They can then be integrated anew into a unitary motion more easily because smaller directional differences make motion integration more likely. Under the "Bidirectional Surround" condition in which no net motion occurs in the surround region, the central region does not contain induced motion that interacts with actual motions. The absence of induced motion in this case was confirmed in a previous study in which a stationary dot did not appear to move in any direction when two background inducers moved in opposing directions (Murakami, 1999). Therefore, a model of this type explains the perception of larger directional differences in the "Same Surround" condition as well as a higher probability of seeing one motion in the "Opposite Surround" condition.

Yet another idea is to consider not addition but suppression of motion signals. Previously, Kim and Wilson (1997) proposed a model assuming such suppression to explain the effect of surrounding motion on the perceived directional shift of a central stimulus. In the model, the surrounding motion suppresses direction-selective motion processing units with a preference for the direction of the surrounding motion. Through such suppression, the representation of motion direction in the center is biased toward the direction opposite the surrounding motion. As a consequence, the perceived direction of the central stimulus, which is physically moving in a direction close to that of the surrounding motion, is biased away from the direction of the surrounding motion. This idea is in line with previous studies of the effect of motion adaptation on the perceived direction of a moving test stimulus (direction aftereffect; Curran, Clifford, & Benton, 2006; Curran et al., 2009; Levinson & Sekuler, 1976; Wilson & Kim, 1994). In the "Same Surround" condition used in the present study, the direction that is "suppressed" is identical to the average between the central two motions. According to the reports of previous studies, such suppression biases the perceived directions away from the vertical direction. Consequently, the perceived directional difference of the central two motions becomes larger. Again, the model also accounts for the higher probability of perceiving one motion under the "Opposite Surround" condition if it is assumed that suppression by the surrounding motion raises the oblique motions steeper than they actually are, making motion integration more likely. What suppression occurs in the "Bidirectional Surround" condition? The simultaneous presence of upward and downward motions in the surround might suppress both upward and downward directions equally in the center. What perception would arise then? Previously, Grunewald and Lankheet (1996) demonstrated that one perceives bidirectional motion aftereffects in orthogonal directions from the adapting directions after adaptation to adapting stimuli moving in opposing directions. They explained this phenomenon by broadly tuned inhibition among direction-selective units elicited by motion adaptation such that when vertical directions are inhibited, horizontal directions become dominant. In contrast, bidirectional induced motions are not elicited in a stationary stimulus by inducers moving in opposing directions in the surround (Murakami, 1999).

Accordingly, we consider that the suppressive effect of two superimposed motions in the "Bidirectional Surround" condition is weaker than that observed in Grunewald and Lankheet's motion aftereffect study, even if it exists. Even if it existed, the "Same Surround" condition (see Figure 2, 100% dots moving upward, making a stronger suppressive impact on oblique-upward motions) would still yield a larger directional difference than the "Bidirectional Surround" condition (only 50% dots moving upward, and the remaining 50% dots moving downward, thus having less suppressive power), and also the "Opposite Surround" condition (biasing toward upward) would still yield a higher probability of motion coherence than the "Bidirectional Surround" condition (possibly biasing toward horizontal), at least within the range of directional differences (up to ±45 deg) of the central stimulus we tested. Still, the idea of bidirectional suppression is in accordance with the actual data (e.g., Figure 6) related to perceived directions (±56.7 deg from the vertical) being biased toward the horizontal than actual (±45 deg) under the "Bidirectional Surround" condition. Deviation from actual directions can be accounted for by directional repulsion, but bidirectional suppression from the vertical bidirectional inducers might enhance biases toward the horizontal directions.

Because the last two ideas are not mutually exclusive, induced motion can have both of these characteristics: the excitation of motion processing units tuned to the motion direction opposite the surrounding motion and the suppression of units tuned to the motion direction of the surrounding motion.

Conclusion

In this study, we demonstrated that the perceptions of motion coherence and transparency change depending on the perceived directions modulated by surrounding motion. This finding suggests that the visual system determines whether an incoming stimulus should be treated as coherent motion or transparent motion based on the internal representation of motion directions, which can be altered by spatial interactions, with the direction of induced motion as a biasing factor. The present results support the view that the perceptions of motion coherence/transparency and induced motion are mediated by mutually communicating mechanisms or even by a common one rather than by independent mechanisms without mutual interference.

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