Vision Research 50 (2010) 2381–2390

Contents lists available at ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

Motion signals deflect relative positions of moving objects

Eiji Watanabe [a,*], Wataru Matsunaga [a], Akiyoshi Kitaoka [b]

[a] *Laboratory of Neurophysiology, National Institute for Basic Biology, Aichi, Japan*
[b] *Department of Psychology, Ritsumeikan University, Kyoto, Japan*

ARTICLE INFO

Article history:
Received 18 May 2010
Received in revised form 17 August 2010

Keywords:
Flash-lag effect
Line motion
Prediction
Postdiction
Kebab illusion
Ambiguous apparent motion
Delta model

ABSTRACT

The perceived relative position of a moving object is frequently shifted as compared to the relative position of the object in the real world. The illusions have traditionally been explained by temporal models that influence the perceptual latency of visual objects. However, another compelling theory has recently been proposed on the basis of spatial models that directly influence the coded location of visual objects. In this study, spatial models were further supported by three different types of illusions composed of apparent motions, in which the perceived relative positions of stationary but apparently moving objects were shifted. One of three illusions was developed as a novel type of illusion in this paper (kebab illusion). The relative position shift of a stationary object suggested that spatial models play important roles on assignment of position of moving object as well as temporal models. A mechanism that integrated temporal and spatial models is also discussed.

1. Introduction

The perceived relative position of a moving object is frequently shifted as compared to the relative position of the object in the real world. Such illusory phenomena have been explored for understanding how the visual system localizes a moving object (Whitney, 2002). For example, a stationary flashed object is perceived to lag behind a spatially aligned moving object (the flash-lag effect; Brenner, Smeets, & van den Berg, 2001; Hazelhoff & Wiersma, 1924; MacKay, 1958; Mateeff & Hohnsbein, 1988; Nijhawan, 1994, 2001; Sperling, 1966; van Beers, Wolpert, & Haggard, 2001), when a moving object appears abruptly from behind a static aperture, the object's initial position seems to be shifted in the direction of motion (the Fröhlich effect; Fröhlich, 1923), and when a moving object vanishes abruptly, an observer's memory of the final position of the previously viewed moving object is displaced forward in the direction of motion (the representational momentum; Freyd & Finke, 1984).

How does the visual system assign the relative positions of moving objects under these circumstances? Two major classes of models for the explanation of the relative position shift of the moving object have been proposed (temporal and spatial models, Fig. 1). In temporal models, the perceived relative position of the moving object depends on the latency of visual processing (Fig. 1B). It assumes that the visual signals of different objects are processed at different latencies. When the processing latency is short, the perceived relative position of the moving object is close to the relative position of the object in the real world at the same time. In spatial models, the visual system directly shifts the apparent location of the moving object in the direction of its motion (Fig. 1C). It assumes that the motion signals directly influence the coded position of the moving object before the perception. In spatial models, the perceived relative position of the moving object can coincide with the relative position of the object in the real world at the same time, in principle.

One of the early examples suggesting the temporal models is the Hess effect (Hess, 1904): when two physically aligned objects of differing brightness move in tandem, the brighter object appears to lead the dimmer object (Hess, 1904; Wilson & Anstis, 1969; Zanker, Quenzer, & Fahle, 2001). Most discussions on the Hess effect have concluded that the abovementioned illusion is due to the different processing times required to perceive objects of different luminance contrasts (Kitaoka & Ashida, 2007; Williams & Lit, 1983). Recently, temporal models have been applied to the explanation of the flash-lag effect (please refer to a review, Whitney, 2002). A representative of the temporal models of the flash-lag effect is the differential latency hypothesis (Purushothaman, Patel, Bedell, & Ogmen, 1998; Whitney & Murakami, 1998) that states that the flash-lag effect occurs simply because the visual system responds with a shorter latency to a moving object than to a flash stimulus. Sampling (Brenner & Smeets, 2000), asynchronous feature binding (Cai & Schlag, 2001), attention (Baldo & Klein, 1995), and misbinding (Gauch & Kerzel, 2008; Kanai, Carlson, Verstraten, & Walsh, 2009) theories also suggest temporal models. A temporal model was also used for explaining the Fröhlich effect (Metzger,

---

* Corresponding author. Address: Laboratory of Neurophysiology, National Institute for Basic Biology, Higashiyama 5-1, Myodaiji-cho, Okazaki, Aichi 444-8787, Japan. Fax: +81 564 55 5596.

E-mail address: eiji@nibb.ac.jp (E. Watanabe).

0042-6989/$ - see front matter © 2010 Elsevier Ltd. All rights reserved.
doi:10.1016/j.visres.2010.09.021

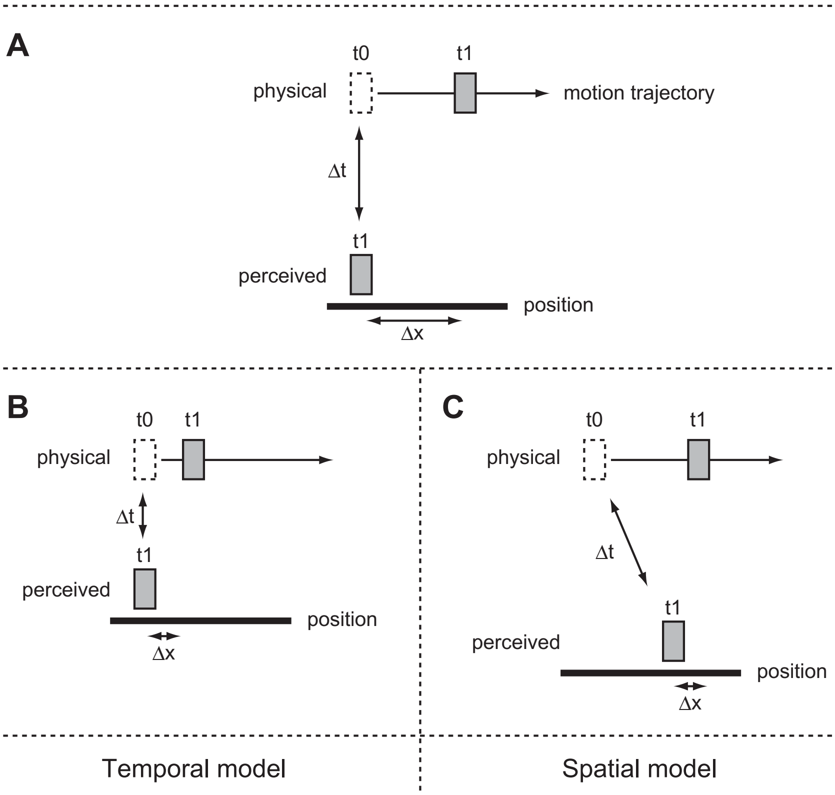

Fig. 1. Temporal and spatial models for localization judgment of moving object. (A) A moving object occurs at time t_0 and is perceived at time t_1. Latency of t_0 and t_1 is shown as Δt. Δx indicates the difference in relative positions of the real object and the perceived object at t_1. (B) Temporal models assume the differential latencies of visual objects. Each visual object has a different latency, whose length depends on the features of the object. When temporal models are applied to the perception of a moving object, Δt influences Δx. B represents shortened Δt in comparison with Δt in A. In such case, Δx becomes reduced. (C) Spatial models propose that the visual system directly operates Δx. Each visual object has a different Δx, whose length depends on the features of the object. C represents shortened Δx in comparison with Δx in A, but the length of Δt is not changed.

1932; Aschersleben & Musseler, 1999; Kirschfeld & Kammer, 1999; Musseler & Aschersleben, 1998; Musseler & Neumann, 1992) and the vernier misalignment of rotating line segments (Martin, Boff, & Pola, 1976).

Historically accumulated data have strongly supported temporal models. However, spatial models have been developed on the basis of several illusory phenomena related to the relative position shift of a moving object. In the related illusory phenomena, the motion signals near a stationary object change the relative position of the stationary object as follows. The apparent position of a physically stationary aperture or window appears to be displaced in the direction of the enclosed moving texture (De Valois & De Valois, 1991; Ramachandran & Anstis, 1990). Snowden (1998), Nishida and Johnston (1999) and Whitaker, McGraw, and Pearson (1999) showed that the motion aftereffect affects the perceived position of the spatial stationary windmill pattern. Surprisingly, the perceived location of a stationary solid bar is influenced by motion signals that originate in the distant regions of another object (Shim & Cavanagh, 2004; Whitney & Cavanagh, 2000). The aperture and window, the windmill pattern, and the solid bars that appear to be displaced in the direction of motion are physically stationary; therefore, there is no latency difference to be measured. In turn, no temporal model can explain why the stimulus appears to be shifted in position, suggesting that the visual system employs spatial models in which the assigned location of the object is directly influenced by the motion signals.

Although the flash-lag effect could be due to the temporal models as described earlier, the illusion may be due to a mechanism that operates strictly in spatial terms. Nijhawan (1994) proposed the motion extrapolation hypothesis, which posits that the visual system uses motion signals to extrapolate the position of a moving object. The mechanism is predictive and bases its computations on the past trajectory of the moving object when a position judgment has to be made. A spatial model was also indicated by the “postdiction” theory, which states that the position of a moving object is determined as a function of what happens approximately 80 ms after the flash onset (Eagleman & Sejnowski, 2000, 2007). This mechanism is “postdictive” and bases its computations on the future trajectory of the moving object. In addition, spatial models have been suggested in the temporal averaging model, which states that the visual system simply averages the position of moving object by the post-flash information (Krekelberg & Lappe, 2000). However, the spatial models have not been sufficiently agreed upon with respect to the relative position shift of a moving object (refer to a special debate in Nijhawan, 2008).

In this paper, we provide further evidence supporting the use of spatial models for explaining the relative position shift of a moving object. Three types of tasks were attempted in this study: (1) a task in which the starting position of a moving object was compared with the subsequent position of the moving object, (2) a task in which the position of one moving object was compared with the position of another moving object, and (3) a task in which the position of a moving object was compared with the position of a flashed object aligned with the moving object (the flash-lag effect). The three types of tasks were respectively utilized three different types of apparent motions. The present study will provide further evidence supporting the idea that spatial models play an important role with respect to the assignment of the position of a moving object as well as temporal models.

2. General method

Stimuli were presented in a moderately darkened room (3 cd m^{-2} on average) on a 17-in cathode ray tube (CRT) monitor (Eizo Nanao, Ishikawa, Japan; viewing area: 31 cm × 23 cm, visual angle: 27.3° × 21.0°) with a refresh rate of 75 Hz and a resolution of 1280 × 1024 pixels. The monitor was gamma-corrected by a software application (Adobe gamma, Adobe systems, San Jose, CA), and spatially calibrated by manual operation. All the stimuli on the monitor were controlled by a Windows PC with a graphics-accelerator card (GeForce 6600, nvidia, Santa Clara, CA) running the Psychlops C++ library for developing a psychophysical stimulus (refer to http://visiome.neuroinf.jp/). The visual stimuli were white (80 cd m^{-2}) and displayed on a gray background (2 cd m^{-2}). The subjects sat comfortably in a chair in front of the computer screen at a viewing distance of 60 cm, with their heads partially immobilized in a chinrest (Handaya, Tokyo, Japan). The viewing was binocular. The subjects were asked to fixate on a position of a white cross subtended 0.15° on each arm, located at the center of the screen. All luminance measures were recorded with a ColorCALII luminance probe (Cambridge Research Systems, Kent, England).

3. Experiment 1: relative position shift of a moving object in a line-motion effect

In the present study, three types of tasks were respectively attempted with three types of apparent motions. In Experiment 1, we attempted a task in which the starting position of a moving object was compared with the subsequent position of the moving object. For this task, we newly developed the relative position shift of a moving object by using the line-motion effect. The line-motion effect occurs in a two-frame sequence: when a flash object (pre-cue) precedes a static line object, an illusory motion perception is observed with a line propagating away from the position of the pre-cue toward the opposite side (Hikosaka, Miyauchi, & Shimojo, 1993). It was reported that the effect resulted from certain types of apparent motion from the pre-cue to the line (Downing & Treisman, 1997; Kawahara, Yokosawa, Nishida, & Sato, 1996); the pre-cue and the line were respectively comparable to the onset and offset of a motion. Therefore, we performed a task in which the starting position (pre-cue) of an apparently moving object was compared with the subsequent position (line) of the object. To easily distinguish the position of the pre-cue from the position of the line, the vertical length of the pre-cue was extended as compared to the conventional line motion stimuli.

3.1. Method

Seven subjects (age group: 22–46 years) participated in the experiment; one of the subjects was the author EW. The remaining six subjects were unaware of the purpose of the experiment. Each had normal or corrected-to-normal vision.

The schematic representation of the stimulus is given in Fig. 2A. The pre-cue was a rectangle subtended 0.75° in height and 0.25° in width, and the target line was subtended 0.25° in height and 3.5° in width. The pre-cue was presented just above the center of the screen. The vertical center of the target line was set to the vertical center of the pre-cue. The line was presented at right or left side of the pre-cue. The position of line (left or right) was counterbalanced and randomly mixed across trials. When the line was presented at the right, the left edge of line was adjusted to the left edge of pre-cue (refer to Fig. 2B, middle box). When the line was presented at the left, the right edge of line was adjusted to the right edge of pre-cue.

A key press by the subject initiated the test; the white fixation cross was presented for 0.5 s after a 1.0-s delay. Next, the pre-cue was presented for 1 video frame (approximately 13.3 ms) after a 1.5-s delay. Then, the target line was presented for 1 video frame with a randomly selected interstimulus interval (ISI) of 0, 1, 2, 3, 4, 5, or 6 video frames. To diminish the influence of the nearby white fixation cross on the localization judgment by subjects, the cross disappeared while the pre-cue and the target line were presented. Our preliminary study confirmed the illusory effect even when the fixation cross was presented all the while. After the line presentation, subjects indicated by pressing one of the two keys on a keyboard whether the side edge of the pre-cue (left edge when the line was presented at the right; right edge when the line was presented at the left) was seen outside (including aligned) or inside of the side edges of the line (refer to Fig. 2B, a two-alternative forced choice task). In another experiment using the same stimuli, subjects indicated by pressing one of the two keys on a keyboard whether the line appeared simultaneously (stasis) or with motion (refer to Fig. 2C). The time to answer was not limited. The subjects carried out 24 trials for each ISI condition, and the data for each ISI condition were averaged for all subjects.

3.2. Results and discussion

The percentage of trials in which the pre-cue appeared to be presented inward with respect to the line was considered the occurrence frequency of the illusion (Fig. 2D, filled circles). The occurrence frequency of the illusion was not significantly different from zero at an ISI of 0 video frames (0 ms) as indicated by the confidence interval ($t(6) = 1.26$, $p = 0.25$, one-tailed t-test). At all other ISIs, the occurrence frequency of the illusion was significantly different from zero (ISI = 1 video frame, $t(6) = 3.63$, etc., $ps < 0.01$). The illusion started to build up at an ISI of 1 video frame and reached a plateau at around 4 video frames (approx. 53.3 ms). Here, this illusion is termed the “kebab” illusion (kebab is a meat dish that is typically cooked with spit or skewer, refer to http://en.wikipedia.org/wiki/Kebab), because the illusion looks like a meat (pre-cue) threaded on a skewer (line; refer to Fig. 2B, inside).

Next, the subjects judged the presence of motion perception on the line (the line-motion illusion) using the same visual stimuli as the kebab illusion. The percentage of trials in which the line appeared to be drawn from the pre-cue side was considered the occurrence frequency of the illusion (Fig. 2D, open circles). As in the case of the kebab illusion, the occurrence frequency of the illusion was significantly different from zero at most ISIs (ISI = 1 video frame, $t(6) = 11.88$, etc., $ps < 0.001$) except in the case of 0 video frames ($t(6) = 1.79$, $p = 0.06$), as indicated by the confidence interval. The illusion started to build up at an ISI of 1 video frame and reached a plateau at around 2 video frames (approx. 26.7 ms). At least within the ISI used in the present study, the presence or absence of the line-motion illusion coincided well with the kebab illusion.

These data clearly indicate that the location of the pre-cue probably shifts in the direction of the illusory motion. The kebab illusion appears to be related to the position shifts from the transformational apparent motion (Whitney, 2006). The transformational apparent motion is an illusion class extended from the line motion and uses “pre-cue” and “line” with a variety of shapes in a two-frame sequence (Tse & Logothetis, 2002). Whitney reported that the relative positions of the flash stationary objects inserted between the two frames shifted in the direction of the perceived motion. In both cases of the kebab and Whitney’s illusions, the similar apparent motions induced the relative position shift of objects. However, the kebab illusion appears to be a novel type of illusion, because the kebab illusion occurred in the localization judgment of apparent “moving” objects, but the relative position

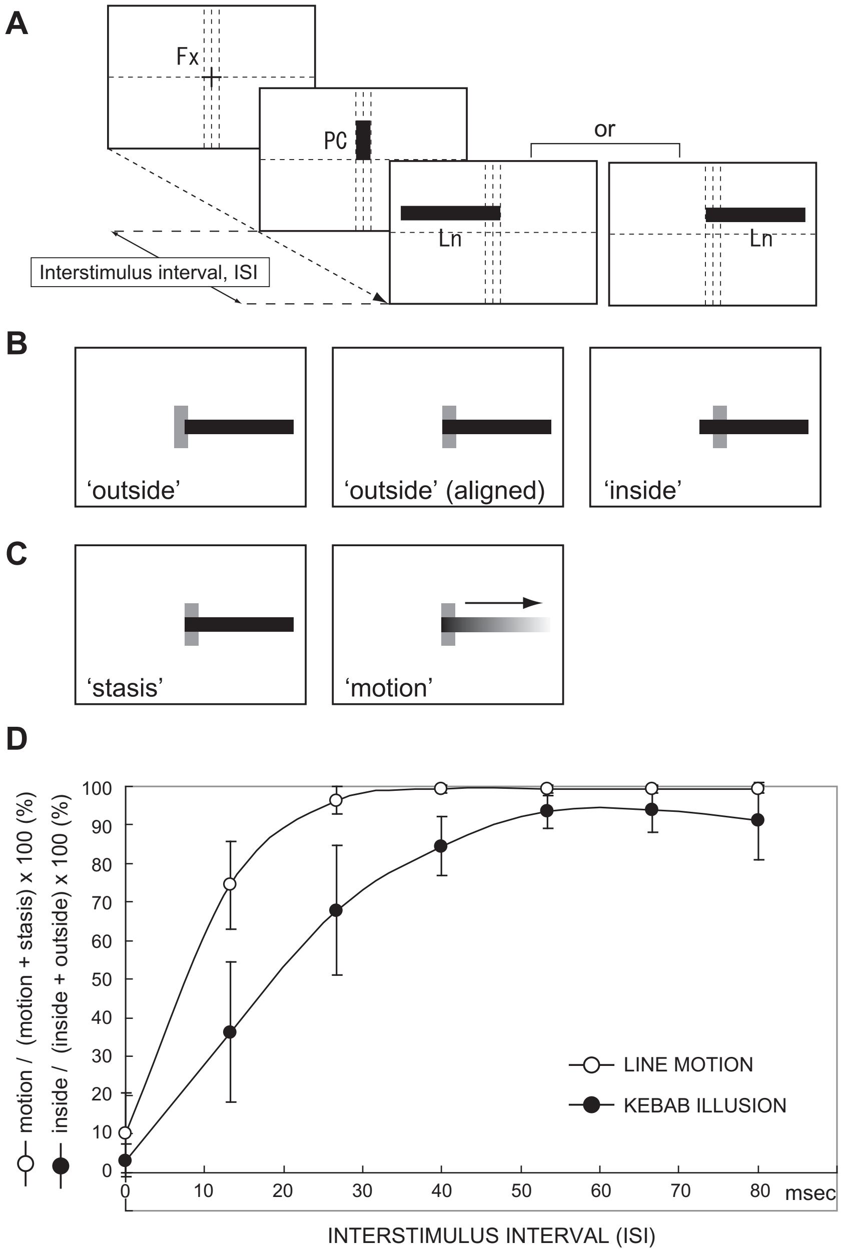

Fig. 2. Experiment 1, kebab illusion. (A) The subject was fixating a central cross (Fx). At a certain time after the disappearance of the fixation cross, a vertical bar (pre-cue, PC) appeared at the center. After a randomized time interval (interstimulus interval, ISI), a line (Ln) was presented at the left or the right side of the visual fields. Dashed lines in the visual fields were not displayed in the actual experiments. (B and C) The subject judged whether the pre-cue was distributed on the outside (including aligned) or inside of the line (kebab illusion, B), or whether the line appeared simultaneously (stasis) or with motion (line motion, C). Gray bars indicate the pre-cue, and solid bars indicate the line. (D) The occurrence frequency of the illusion (please refer to ordinate in detail) was plotted against the lead time of the pre-cue object (abscissa). Data of the kebab illusion is shown by closed circles, and data of the line-motion effect is shown by open circles. Data from seven subjects are shown as mean ±95% confidence interval. Twenty-four trials were obtained for each lead time of a pre-cue in each subject.

shift of "stationary" objects was induced by another moving object in Whitney's illusion. When a moving object vanishes abruptly, an observer's memory for the final position of a previously viewed moving object is often displaced forward in the direction of motion (the representational momentum; Freyd & Finke, 1984). The representational momentum also differs from the kebab illusion as the motion in the kebab illusion is preceded by the flash object, whose position is compared with that of the subsequent moving object. Therefore, the kebab illusion can also be called "the backward representational momentum."

As indicated above, the line-motion effect was thought to be a result of certain types of apparent motion from the pre-cue to the line (Downing & Treisman, 1997; Kawahara et al., 1996). When this is the case, the pre-cue and the line act as if they are parts of a single moving object. Considering our stimuli in the same way (as Kawahara, Yokosawa, Nishida, & Sato, 1996; Downing & Treisman, 1997), an illusory position-shift effect inside a single moving object should be noted as one of the novelties of the kebab illusion.

The illusory line motion was originally described as a measure of the facilitatory effects of a visual attention gradient (Hikosaka et al., 1993). Focal attention accelerates visual processing locally, and hence, visual signals reach the motion detector sequentially, as in the case of real motion. However, the acceleration of visual processing by focal attention cannot explain the position shift of the pre-cue in the kebab illusion.

4. Experiment 2: relative position shift of a moving object in an ambiguous apparent motion

In the present study, three types of tasks were respectively attempted in three types of apparent motions. In Experiment 2, we attempted a task in which the position of one moving object was compared with the position of another moving object aligned with the former moving object. An ambiguous apparent motion was constructed by four square-shaped objects with the same size and located at the four vertices of a lozenge. A pair of objects aligned vertically was onset or offset of the apparent motion, and another pair of objects aligned horizontally was the offset or the onset, respectively (please refer to Fig. 3A and Section 4.1 in detail). The test stimuli potentially generate four motions—two up-motions and two down-motions. However, subjects simultaneously perceived only two motions—one up-motion and another down-motion located at diagonal position of the up-motion—from among these four motions. Then, we tested a task in which subjects compared the relative starting (onset) position of two apparently moving objects aligned vertically. In another task, subjects compared the ending (offset) positions of two apparently moving objects aligned vertically.

4.1. Method

Six subjects (age group: 22–46 years) participated in the experiment; one of these subjects was the author EW. The remaining five subjects were unaware of the purpose of the experiment. Each had normal or corrected-to-normal vision.

We prepared two types of stimuli of an ambiguous apparent motion (onset and offset conditions; schematically illustrated in Fig. 3A). In all conditions, a key press by the subjects initiated a pilot stimulus followed by a test stimulus. In the test stimulus of the onset condition, a pair of white squares (0.25° on a side) placed above and below the cross position (vertical distance of 2.0°, center to center) were presented for 1 video frame (approx. 13.3 ms) after the cross presentation, as described above. To diminish the influence of the nearby white fixation cross on the localization judgment by subjects, the cross disappeared while the squares were presented. Our preliminary study confirmed the illusory effect even when the fixation cross was presented all the while. The horizontal position of each square was randomly selected ($-0.072°$, $-0.048°$, $-0.024°$, 0°, 0.024°, 0.048°, and 0.072° from the vertical center). The two squares were arranged on the opposite angle across the cross. As a result, horizontal distances between the two squares were $-0.144°$, $-0.096°$, $-0.048°$, 0, 0.048°, 0.096°, and 0.144° with respect to the position of each square. Next, a pair of white squares (0.25° on a side) placed on the left and the right of the cross position (horizontal distance of 3.0°, center to center) were presented for 1 video frame after a 5-video-frame (approx. 66.7 ms) delay. The positions of the pair of squares presented later were fixed.

In order to reinforce that subjects select one motion set (one down-motion and one up-motion) from the two potential motion sets (two down-motions and two up-motions), the subjects were introduced to pilot stimuli in each trial prior to the test stimuli. For a pilot stimulus, a square above the cross was presented for 1 video frame at first, and then, one square randomly selected from the two squares on either side of the cross was presented for 1 video frame after a 5-video-frame delay. After a 400-ms duration, a square below the cross was presented for 1 video frame, and then, a square on another side of the cross was presented after a 5-video-frame duration. This pilot stimulus was repeated three times with a 400-ms interval. The interval between a pilot and a test stimulus was 1.6 s. The positions of the squares in a pilot stimulus were the same as those in a test stimulus. The motion direction in a pilot stimulus was randomly selected, and the number of squares in each direction was counterbalanced. In a two-alternative forced choice (2AFC) task, subjects had to judge whether the position angles of two vertical squares were right-handed or left-handed. There were 20 trials for each position and a total of 140 (20×7) trials for each subject. In the offset condition, the pair of squares aligned horizontally were presented first, and the pair of squares aligned vertically were presented subsequently. Point of subjective equality of each subject was calculated by a Probit analysis (Finney, 1971) and averaged.

4.2. Results and discussion

The positive value of the magnitude of the illusion was defined as a position shift in the direction of motion (please refer to Fig. 3C); the "left or right" response of the subject was translated into a "positive or negative" value according to the direction of motion of each test stimulus. The illusion magnitudes of the onset and offset conditions are shown in Fig. 3B. The magnitude was significantly larger in the onset condition than in the offset condition ($t(5) = 2.18$, $p < 0.05$). In one of the subjects, the magnitude was smaller in the onset condition than in the offset condition. The illusion magnitude was significantly different from zero in the onset condition as indicated by the confidence interval ($t(5) = 3.35$, $p < 0.01$), but did not differ in the offset condition ($t(5) = 0.52$, $p = 0.31$).

The data clearly indicated that each starting object shifted in the motion trajectory (onset) and that each ending object did not shift in the motion trajectory (offset). If the onset condition is regarded as a stroboscopic Fröhlich effect and the offset condition is regarded as a stroboscopic representational momentum, the data can be interpreted as the stroboscopic Fröhlich effect was observed but the stroboscopic representational momentum was not observed.

In this experiment, since pilot stimuli were presented 1.6 s before the test stimuli, the motion aftereffect (Wohlgemuth, 1911) induced by the pilot stimuli could occur during the test stimuli to a greater or lesser extent. The underestimated effect of the test stimuli induced by the motion aftereffect in the opposite direction of the apparent motion must be taken into account.

In a related illusion to that in Experiment 2, the position capture effect induced by the bistable quartet motion was studied by Shim and Cavanagh (2004). In their experiments, the influence of the bistable quartet motion on the perceived position of the nearby stationary objects was studied. It was found that an illusory position shift was observed only when the flashes were adjacent to the path where motion was perceived. While the illusory effect of Experiment 2 is involved in an issue of the relative position of a moving object, the position capture effect is involved in an issue of the relative position of a stationary object away from the motion. The position comparisons were performed between stationary objects in both studies; therefore, it is difficult for enhanced or lagging visual processing to explain the illusory position shift of stationary objects emerged in ambiguous apparent motions.

5. Experiment 3: flash-lag effect by a simplistic apparent motion

In the present study, three types of tasks were respectively attempted in three types of apparent motions. In Experiment 3, we attempted a task in which the position of one moving object was compared with the position of a flashed object aligned with the moving object (the flash-lag effect). The stimuli were constructed by square-shaped objects with the same size. The use of objects with the same symmetrical shape potentially induced variant

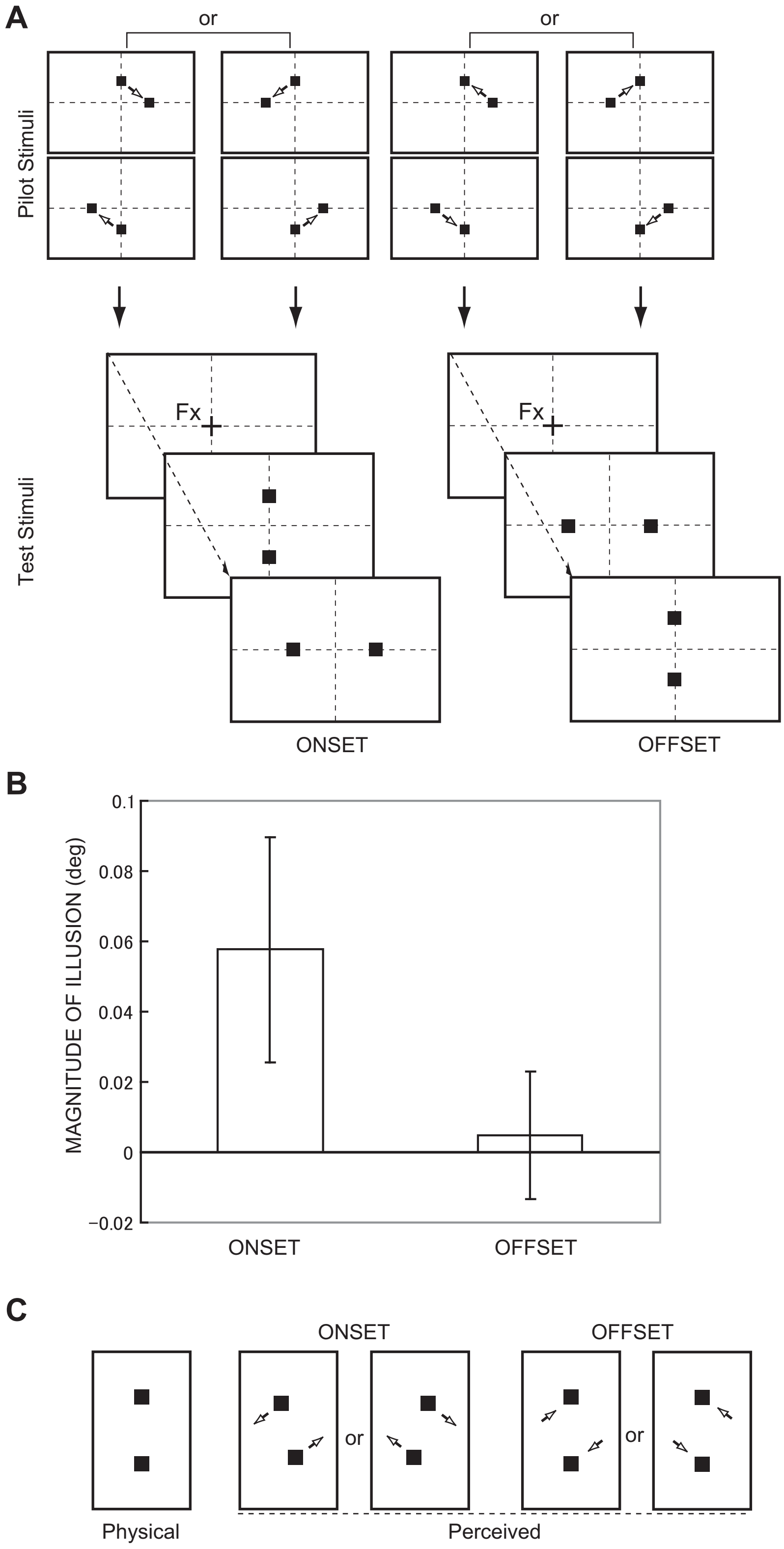

Fig. 3. Experiment 2, illusory mislocation of a motion object in an ambiguous apparent motion. (A) In order to reinforce that the subjects select one motion set (one down-motion and one up-motion) from two potential motion sets (two down-motions and two up-motions), pilot stimuli were introduced in each trial prior to the test stimuli. After the introduction of the pilot stimuli, the subject fixated a central cross (Fx). At a certain time after the disappearance of the fixation cross, a pair of squares arranged above and below (onset) or left and right (offset) of the center of the display was presented. At a certain time after the disappearance of the pair of squares, another pair of squares arranged left and right (onset) or above and below (offset) of the center of display was presented. The subjects judged whether the position angles of two vertical squares were right-handed or left-handed. The positive value of the magnitude of illusion was defined as the position shift in the direction of motion. The point of subjective equality was determined as the measure of the perceived mislocation for each subject. (B) The magnitude of illusion in the onset and offset conditions is shown. Data from six subjects are shown as mean ±95% confidence interval. (C) A schematic representation of the illusion. Starting objects (onset), but not the ending objects (offset), of the ambiguous apparent motion are perceived to be shifted to the subjective motion direction. White arrows indicate the directions of apparent motion.

motions in the atypical diagonal trajectories (dashed arrows in Fig. 4C) in addition to the horizontal trajectory (The subjects were instructed to note the horizontal motion in this experiment.). In the past experiments of the flash-lag effect, the two objects were presented as different shapes in order to prevent an ambiguity between the flash and the motion objects. In exchange for the ambiguity, the look-alike features of apparently moving and flashed objects in Experiment 3 most likely reduced the differential latency of the visual processing of the two objects. Then, we examined the magnitudes of the flash-lag effect in the onset, offset, conventional flash-lag, and reverse conditions.

5.1. Method

Six subjects (age group: 22–46 years) participated in the experiment; one of these subjects was the author EW. The remaining five subjects were unaware of the purpose of the experiment. Each had normal or corrected-to-normal vision.

The schematic representation of the four conditions (onset, offset, flash-lag, and reverse) used in this experiment is given in Fig. 4A. The flashed and apparently moving objects were white squares of the same size (0.5° on a side). In all conditions, a key press by the subject initiated the trial, and then, a fixation cross

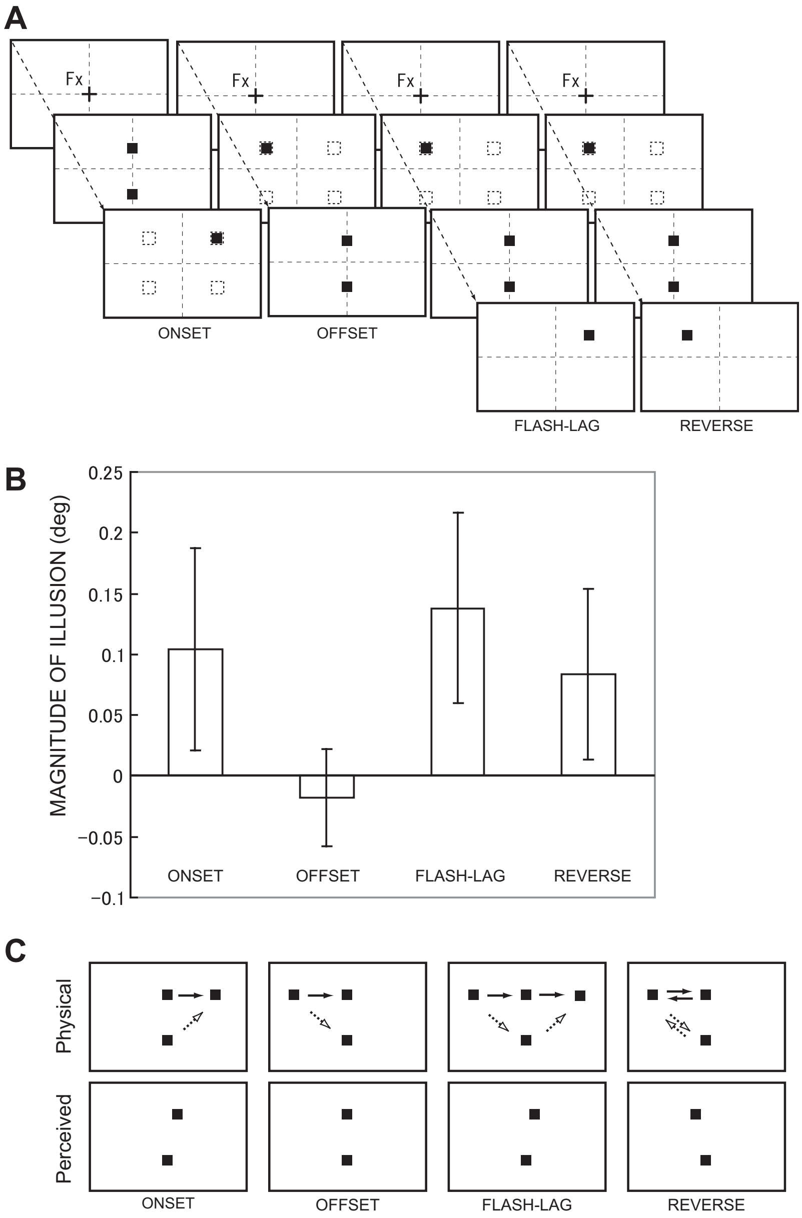

Fig. 4. Experiment 3, flash-lag effect of a simplistic apparent motion. (A) The subject fixated a central cross (Fx). After the disappearance of the fixation cross, sets of test stimuli were presented in each condition: onset, offset, flash-lag, and reverse conditions. In the onset condition, a pair of squares that was arranged above and below the center of the screen and a following object that was randomly selected from four positions (dashed boxes) were presented successively. In the offset condition, a leading object that was randomly selected from four positions (dashed boxes) and a pair of squares that was arranged above and below the center of the screen were presented successively. In the flash-lag condition, a leading object that was randomly selected from four positions (dashed boxes), a pair of squares that was arranged above and below the center of the screen, and the last object located at the opposite side of the leading object were presented successively. In the reverse condition, a leading object that was randomly selected from four positions (dashed boxes), a pair of squares that was arranged above and below the center of the screen, and the last object located at the same position of the leading object were presented. In a two-alternative forced choice (2AFC) task, subjects judged whether an apparently moving square at the center led the flash square at the center. The point of subjective equality was determined as the measure of the perceived mislocation for each subject. (B) The magnitudes of illusion in the four conditions are shown. Data from six subjects are shown as mean ±95% confidence interval. (C) A schematic representation of the illusion. Subjects were instructed to note the horizontal motion (solid arrows). Dashed arrows indicate the potentially perceivable motions caused by the use of the same square-shaped objects. The flash-lag effect was observed under conditions other than the offset condition.

appeared after a 1.0-s delay. The cross was presented for 1.0 s; then, the square(s) appeared after a 0.5-s delay. To diminish the influence of the nearby white fixation cross on the localization judgment by subjects, the cross disappeared while the squares were presented. Our preliminary study confirmed the illusory effect even when the fixation cross was presented all the while. Subjects were asked to fixate on the position of the white cross during each trial.

In the flash-lag condition, the apparently moving squares occupied three positions over 9 video frames (approx. 120 ms, each presentation of 1 video frame and each interval of 3 video frames); these squares were arranged on a horizontal plane at equal intervals (4.32°, center to center). The apparently moving squares at the second position and a flashed square appeared simultaneously at the horizontal center of the screen. The apparently moving squares were presented at fixed positions, whereas the horizontal position of the flashed square was randomly selected (0.192°, 0.144°, 0.096°, 0.048°, 0°, −0.048°, −0.096°, −0.144°, −0.192°, −0.24°, and −0.288°; the plus sign indicates the motion direction). The vertical distance between the flash square and the fixation cross was the same as that between the apparently moving square of the second position and the fixation cross (2.3° each). The first apparently moving square appeared to be randomly selected from the left-top, the left-bottom, the right-top, or the right-bottom squares (dot-lined boxes in Fig. 4A). In other words, the apparently moving and flashed objects changed places at random. In a two-alternative forced choice (2AFC) task, the subjects had to judge whether an apparently moving square at the second position led the flash square. There were 20 trials at each position and a total of 220 (20 × 11) trials for each subject. In the reverse condition, the third apparently moving square was returned to the first position. In the offset condition, the third apparently moving square was omitted. In the onset condition, the first apparently moving square was omitted. Point of subjective equality of each subject was determined as described above and averaged.

5.2. Results and discussion

The position shift in the motion direction was defined as the positive illusion. In the case of the reverse condition, the position shift in the last motion direction was defined as the positive effect. The illusion magnitude was not significantly different from zero at the offset condition as indicated by the confidence interval ($t(5) = -0.89$, $p = 0.21$). In the case of all other conditions, it was significantly different from zero (onset, $t(5) = 2.45$, $p < 0.05$; flash-lag, $t(5) = 3.46$, $p < 0.01$; reverse, $t(5) = 2.34$, $p < 0.05$). In one subject, the magnitude was smaller in the onset condition than in the offset condition. The differences between the illusions of the offset condition and any one of the other conditions were significant (onset versus offset, $t(5) = 2.14$, $p < 0.05$; flash-lag, $t(5) = 2.94$, $p < 0.05$; reverse, $t(5) = 2.04$, $p < 0.05$); however, no other paired comparisons differed.

The result indicated that the position shift was detected in conditions other than the offset condition. Similar results were reported in a number of previous studies on the flash-lag effect (please refer to a review, Nijhawan, 2008). Several conditions in Experiment 3 were rather similar to the conditions used in studies by Rizk, Chappell, and Hine (2009), in which the flash-lag effects of an apparent motion were studied by using asymmetrical triangles. However, unpredictability in the onset condition of the present visual stimuli should be noted in particular (Fig. 4A, onset). Because the moving object and the flashed object have the same symmetrical shape in the present study, subjects cannot figure out which object is the moving object and which direction is the motion trajectory at the time of onset. Therefore, the present data of onset condition strongly support one of the spatial models, the "postdiction" hypothesis (Eagleman & Sejnowski, 2000, 2007) that postulates that the localization estimate of an object is shifted in the direction of motion signals collected after the emergence of the object.

6. General discussion

Hypotheses to explain the relative position shift of a moving object have been classified roughly into temporal and spatial models, as described in Introduction. Temporal models propose that the illusion is due to the differential times for the information processing of two target objects, whose relative positions are judged by the subjects (Fig. 1B). Recently, the related illusory effects that are difficult to explain by using temporal models have been reported (Whitney, 2002), and spatial models have emerged as the alternative hypothesis. According to the related illusory effects, the relative positions of stationary objects were influenced by motion signals derived from the other objects near the stationary objects. Even if each stationary object has a differential latency for perception, the onset time of perception will vary among them, but that cannot explain the relative position shift of the stationary objects. In contrast, since spatial models assume the existence of information processing to directly edit the coded relative position of a moving object (Fig. 1C), the relative position shift of stationary objects is well explained by spatial models. All the present experiments, Experiments 1, 2, and 3, presented the relative position shift of a stationary object—the stationary pre-cue in Experiment 1 and the stationary square in Experiments 2 and 3. Therefore, these data emphasize the value of further studies on spatial models.

6.1. Onset versus offset

Experiments 2 and 3 indicated that the relative position shift of a moving object preferred onset conditions. The advantage of the onset conditions for the illusory phenomena is also reported in a discussion on the flash-lag effect (Chappell, Hine, Acworth, & Hardwick, 2006; Eagleman & Sejnowski, 2000, 2007; Rizk et al., 2009). The illusory position shift in motion onset was also clearly observed in a study on the Fröhlich effect (Fröhlich, 1923). Why does the illusory position shift tend to occur in onset conditions rather than offset conditions?

The postdiction hypothesis (Eagleman & Sejnowski, 2000, 2007) among spatial models well explains the advantage of the onset conditions in Experiments 2 and 3. Because the postdiction hypothesis bases its computations on the future trajectory of the moving object, the illusory effect does not occur under the offset conditions in which there is no motion in the future. In the kebab illusion, the pre-cue as the onset of motion was shifted in the direction of motion trajectory. Because the subsequent line was presented randomly at the right side or the left side of the display (Fig. 2A), subjects cannot figure out which direction is the motion trajectory at the time of onset. Therefore, the present data of the kebab illusion also support the postdiction hypothesis.

However, the postdiction hypothesis appears not to account for several illusory effects concerning the relative position shift of a moving object. For example, moving objects with ambiguous edges caused a position shift even under the offset condition (Fu, Shen, & Dan, 2001; Soga, Akaishi, & Sakai, 2009). These phenomena were well explained by a combination of the postdiction and the motion extrapolation hypothesis (Soga et al., 2009). The ambiguous stimuli may decrease the accuracy of visual prediction by the postdiction mechanism. Consequently, such specialized offset conditions could elicit the illusory effect by the motion extrapolation mechanism which bases its computations on the past trajectory of the moving object. The representational momentum also showed that the offset position of moving object was shifted in the direction of the motion trajectory (Freyd & Finke, 1984). In the case of the representational momentum, the offset position retained in subject's memory was compared with the position of the subsequently presented stationary object. The time lag of the compared two objects is a potential ambiguity for the subjects, suggesting again a combination of the postdiction and the motion extrapolation hypothesis. Degree of the contribution to the illusory effect is uncertain, but the motion extrapolation hypothesis should not be excluded.

6.2. Temporal models versus spatial models

As described in Introduction, temporal models have been supported by many studies on the relative position shift of a moving object. In addition to motion defined as a temporal change in position, other smoothly changing features such as color, luminance, spatial frequency, pattern entropy (Sheth, Nijhawan, & Shimojo, 2000), and changing words (Bachmann & Poder, 2001) were similarly deflected. The continuously changing item led the flashed item in the feature space. These changing features did not include a retinotopic change in the space; therefore, they should be represented in a temporal framework. Furthermore, electrophysiological studies of the population responses of neurons in the primary visual cortex of a cat also strongly suggest the existence of temporal models (Jancke, Erlhagen, Schoner, & Dinse, 2004). The population response of the primary visual cortex indicated that the latency for a moving stimulus is shorter than the latency for a single flash stimulus. Temporal models should not be excluded, although care should be taken when physiological data are accompanied with visual illusions as a matter of course.

Is it impossible for temporal models to coexist with spatial models? There are clear differences between the two classes of models. Temporal models assume a differential processing time for each object in the visual field. This idea appears to be based on the parallel processing of the visual information. In turn, temporal models operate only on the local information of each object. On the other hand, spatial models operate on the relative position among objects. In turn, spatial models involve the accessing of motion signals over large regions of the visual field. Therefore, it is conceivable that the two classes of models coexist in a complementary fashion. This view emphasizes the necessity for a novel model incorporating both temporal and spatial concepts.

7. Perspective

Although the exploration of novel mechanisms may be beyond the scope of the present study, our conclusion strongly suggests that any models incorporating temporal and spatial models will contribute to future research in this area. We therefore propose a simple conceptual model as follows:

Spatial models suggest that motion signals interpose and alter the position information that is originally derived from sensory organs. Perceived vision appears to be based on this altered position information. Consequently, there exists a second signal other than the "bottom-up" sensory signals closely related to the physical position information. A conceptual model, *delta model*', is shown in Fig. 5. In this model, the "top-down" signals as the second signal representing visual prediction are proposed in addition to the "bottom-up" sensory signals. The delta model hypothesizes subtraction between the two signals, and the resultant difference (delta) as the prediction error enter the "top" that operates the "top-down" signals for the reduction of delta. In the case of the perception of the moving object, Δ represents Δx, as shown in Fig. 1. Spatial models postulating the direct operation of Δx may specifically contribute to the "top-down" signals. In contrast, temporal models postulating the operation of Δt throughout the visual system may contribute to both signals; decrease of Δt is expected to enhance the accuracy of prediction. One of the notable points of the delta model is that delta as an error signal potentially involves error learning on the visual system. This type of learning model has long been proposed in the motor system of the brain (Ito, 2006, 2008; Wolpert, Miall, & Kawato, 1998); the delta represents the prediction error of the motion trajectory planned by the cerebellum. Recent physiological and theoretical studies have also suggested that the reward system of the brain utilizes a similar mechanism (Kobayashi & Okada, 2007; Schultz, 1998; Schultz & Dickinson, 2000); the delta represents the prediction error of the reward expected by the dopamine system. Even in the visual system, a similar mechanism was proposed as a learning theory (Kawato, Hayakawa, & Inui, 1993).

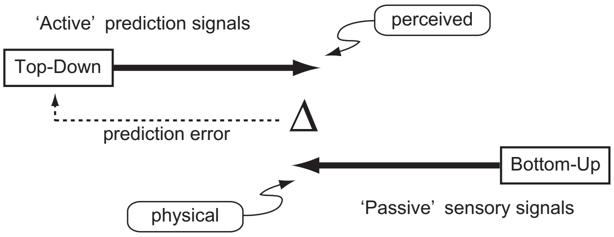

Fig. 5. Delta model. Two types of signals (top-down and bottom-up) are assumed in this model. Top-down signals are hypothesized to be derived from a higher level of the visual system and represent the predictive visual information. Bottom-up signals are hypothesized to be derived from a lower level of the visual system and represent the original sensory information. Subtraction occurs between the two signals; the resultant prediction error (Δ) is input to a higher level of the visual system that operates the top-down signal to minimize the prediction error. In the case of the localization judgment of the moving object, Δ represents Δx as shown in Fig. 1.

One of the main targets of future research in this field will be to clarify how the two types of models—temporal and spatial models—contribute to a variety of mislocalizations induced by visual motion. Given that the two models coexist, more studies are required for exploring an integrated mechanism of visual localization as a delta model that must necessarily explain how the visual system processes motion information and generates our perception.

Acknowledgments

We would like to thank Drs. Hiroaki Kobayashi, Yasushi Kobayashi, and Ayano Nagakura for helpful comments on this manuscript, and Ms. Mie Watanabe for secretarial assistance. This research was supported by the Ministry of Education, Culture, Sports, Science and Technology (MEXT) of Japan.

References

Aschersleben, G., & Musseler, J. (1999). Dissociations in the timing of stationary and moving stimuli. *Journal of Experimental Psychology: Human Perception and Performance, 25*, 1709–1720.

Bachmann, T., & Poder, E. (2001). Change in feature space is not necessary for the flash-lag effect. *Vision Research, 41*(9), 1103–1106.

Baldo, M. V., & Klein, S. A. (1995). Extrapolation or attention shift? *Nature, 378*, 565–566.

Brenner, E., & Smeets, J. B. (2000). Motion extrapolation is not responsible for the flash-lag effect. *Vision Research, 40*(13), 1645–1648.

Brenner, E., Smeets, J. B., & van den Berg, A. V. (2001). Smooth eye movements and spatial localisation. *Vision Research, 41*(17), 2253–2259.

Cai, R., & Schlag, J. (2001). A new form of illusory conjunction between color and shape [Abstract]. *Journal of Vision, 1*(3), 127a.

Chappell, M., Hine, T. J., Acworth, C., & Hardwick, D. R. (2006). Attention 'capture' by the flash-lag flash. *Vision Research, 46*(19), 3205–3213.

De Valois, R. L., & De Valois, K. K. (1991). Vernier acuity with stationary moving Gabors. *Vision Research, 31*(9), 1619–1626.

Downing, P. E., & Treisman, A. M. (1997). The line-motion illusion: Attention or impletion? *Journal of Experimental Psychology: Human Perception and Performance, 23*(3), 768–779.

Eagleman, D. M., & Sejnowski, T. J. (2000). Motion integration and postdiction in visual awareness. *Science, 287*, 2036–2038.

Eagleman, D. M., & Sejnowski, T. J. (2007). Motion signals bias localization judgments: A unified explanation for the flash-lag, flash-drag, flash-jump, and Fröhlich illusions. *Journal of Vision, 7*(4), 1–12.

Finney, D. J. (1971). *Probit analysis* (3rd ed.). Cambridge: Cambridge University Press. 333 p.

Freyd, J. J., & Finke, R. A. (1984). Representational momentum. *Journal of Experimental Psychology: Learning, Memory, & Cognition, 10*, 126–132.

Fröhlich, F. W. (1923). Uber die Messung der Empfindungszeit. *Zeitschrift fur Sinnesphysiologie, 54*, 58–78.

Fu, Y. X., Shen, Y., & Dan, Y. (2001). Motion-induced perceptual extrapolation of blurred visual targets. *Journal of Neuroscience, 21*(RC172), 1–5.

Gauch, A., & Kerzel, D. (2008). Comparison of flashed and moving probes in the flash-lag effect: Evidence for misbinding of abrupt and continuous changes. *Vision Research, 48*(15), 1584–1591.

Hazelhoff, F. F., & Wiersma, H. (1924). Die Wahrnehmungszeit. *Zeitschrift fur Psychologie, 96*, 171–188.

Hess, C. V. (1904). Untersuchungen uber den Erregungsvorgang in Sehorgan bei Kurz- und bei langer dauernder Reizung. *Pflugers Archiv fur die Gesamte Physiologie, 101*, 226–262.

Hikosaka, O., Miyauchi, S., & Shimojo, S. (1993). Focal visual attention produces illusory temporal order and motion sensation. *Vision Research, 33*(9), 1219–1240.

Ito, M. (2006). Cerebellar circuitry as a neuronal machine. *Progress in Neurobiology, 78*(3–5), 272–303.

Ito, M. (2008). Control of mental activities by internal models in the cerebellum. *Nature Reviews Neuroscience, 9*(4), 304–313.

Jancke, D., Erlhagen, W., Schoner, G., & Dinse, H. R. (2004). Shorter latencies for motion trajectories than for flashes in population responses of cat primary visual cortex. *Journal of Physiology, 556*(Pt 3), 971–982.

Kanai, R., Carlson, T. A., Verstraten, F. A., & Walsh, V. (2009). Perceived timing of new objects and feature changes. *Journal of Vision, 9*(7), 1–13.

Kawahara, J., Yokosawa, K., Nishida, S., & Sato, T. (1996). Illusory line motion in visual search: Attentional or apparent motion? *Perception, 25*, 901–920.

Kawato, M., Hayakawa, H., & Inui, T. (1993). A forward-inverse optics model of reciprocal connections between visual cortical areas. *Network, 4*, 415–422.

Kirschfeld, K., & Kammer, T. (1999). The Fröhlich effect: A consequence of the interaction of visual focal attention and metacontrast. *Vision Research, 39*(22), 3702–3709.

Kitaoka, A., & Ashida, H. (2007). A variant of the anomalous motion illusion based upon contrast and visual latency. *Perception, 36*, 1019–1035.

Kobayashi, Y., & Okada, K. (2007). Reward prediction error computation in the pedunculopontine tegmental nucleus neurons. *Annals of the New York Academy of Sciences, 1104*, 310–323.

Krekelberg, B., & Lappe, M. (2000). A model of the perceived relative positions of moving objects based upon a slow averaging process. *Vision Research, 40*(2), 201–215.

MacKay, D. (1958). Perceptual stability of a stroboscopically lit visual field containing self-luminous objects. *Nature, 181*, 507–508.

Martin, L., Boff, K. R., & Pola, J. (1976). Vernier offset produced by rotary target motion. *Perception & Psychophysics, 20*, 138–142.

Mateeff, S., & Hohnsbein, J. (1988). Perceptual latencies are shorter for motion towards the fovea than for motion away. *Vision Research, 28*(6), 711–719.

Metzger, W. (1932). Versuch einer gemeinsamen Theorie der Phanomene Frohlichs und Hazelhoffs und Kritik ihrer Verfahren zur Messung der Empfindungszeit. *Psychologische Forschung, 16*, 176–200.

Musseler, J., & Aschersleben, G. (1998). Localizing the first position of a moving stimulus: The Fröhlich effect and an attention-shifting explanation. *Perception & Psychophysics, 60*, 683–695.

Musseler, J., & Neumann, O. (1992). Apparent distance reduction with moving stimuli (tandem effect): Evidence for an attention-shifting model. *Psychological Research, 54*, 246–266.

Nijhawan, R. (1994). Motion extrapolation in catching. *Nature, 370*, 256–257.

Nijhawan, R. (2001). The flash-lag phenomenon: Object motion and eye movements. *Perception, 30*, 263–282.

Nijhawan, R. (2008). Visual prediction: Psychophysics and neurophysiology of compensation for time delays. *Behavioral and Brain Sciences, 31*(2), 179–198 [discussion 198–239].

Nishida, S., & Johnston, A. (1999). Influence of motion signals on the perceived position of spatial pattern. *Nature, 397*, 610–612.

Purushothaman, G., Patel, S. S., Bedell, H. E., & Ogmen, H. (1998). Moving ahead through differential visual latency. *Nature, 396*, 424.

Ramachandran, V. S., & Anstis, S. M. (1990). Illusory displacement of equiluminous kinetic edges. *Perception, 19*(5), 611–616.

Rizk, J. K., Chappell, M., & Hine, T. J. (2009). Effect of motion smoothness on the flash-lag illusion. *Vision Research, 49*(17), 2201–2208.

Schultz, W. (1998). Predictive reward signal of dopamine neurons. *Journal of Neurophysiology, 80*(1), 1–27.

Schultz, W., & Dickinson, A. (2000). Neuronal coding of prediction errors. *Annual Review of Neuroscience, 23*, 473–500.

Sheth, B. R., Nijhawan, R., & Shimojo, S. (2000). Changing objects lead briefly flashed ones. *Nature Neuroscience, 3*(5), 489–495.

Shim, W. M., & Cavanagh, P. (2004). The motion-induced position shift depends on the perceived direction of bistable quartet motion. *Vision Research, 44*(20), 2393–2401.

Snowden, R. J. (1998). Shifts in perceived position following adaptation to visual motion. *Current Biology, 8*, 1343–1345.

Soga, R., Akaishi, R., & Sakai, K. (2009). Predictive and postdictive mechanisms jointly contribute to visual awareness. *Consciousness and Cognition, 18*(3), 578–592.

Sperling, G. (1966). Comparisons of real and apparent motion. *Journal of the Optical Society of America, 56*, 1442.

Tse, P. U., & Logothetis, N. K. (2002). The duration of 3-d form analysis in transformational apparent motion. *Perception & Psychophysics, 64*(2), 244–265.

van Beers, R. J., Wolpert, D. M., & Haggard, P. (2001). Sensorimotor integration compensates for visual localization errors during smooth pursuit eye movements. *Journal of Neurophysiology, 85*, 1914–1922.

Whitaker, D., McGraw, P. V., & Pearson, S. (1999). Non-veridical size perception of expanding and contracting objects. *Vision Research, 39*(18), 2999–3009.

Whitney, D. (2002). The influence of visual motion on perceived position. *Trends in Cognitive Science, 6*(5), 211–216.

Whitney, D. (2006). Contribution of bottom-up and top-down motion processes to perceived position. *Journal of Experimental Psychology: Human Perception and Performance, 32*(6), 1380–1397.

Whitney, D., & Cavanagh, P. (2000). Motion distorts visual space: Shifting the perceived position of remote stationary objects. *Nature Neuroscience, 3*(9), 954–959.

Whitney, D., & Murakami, I. (1998). Latency difference, not spatial extrapolation. *Nature Neuroscience, 1*(8), 656–657.

Williams, J. M., & Lit, A. (1983). Luminance-dependent visual latency for the Hess effect, the Pulfrich effect, and simple reaction time. *Vision Research, 23*, 171–179.

Wilson, J. A., & Anstis, S. M. (1969). Visual delay as a function of luminance. *American Journal of Psychology, 82*, 350–358.

Wohlgemuth, A. (1911). On the aftereffect of seen movement. *The British Journal of Psychology: Monograph Supplements, 1*, 1–117.

Wolpert, D. M., Miall, R. C., & Kawato, M. (1998). Internal models in the cerebellum. *Trends in Cognitive Sciences, 2*(9), 338–347.

Zanker, J. M., Quenzer, T., & Fahle, M. (2001). Perceptual deformation induced by visual motion. *Naturwissenschaften, 88*, 129–132.