Sustained directional biases in motion transparency

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In motion transparency, one surface is very often seen on top of the other in spite of no proper depth cue in the display. We investigated the dynamics of depth assignment in motion transparency stimuli composed of random dots moving in opposite directions. Similarly to other bistable percepts, which surface is seen in front is arbitrary and changes over time. In addition, we found that helping the segregation of the two surfaces by giving the same color to all dots of one surface significantly slowed down the initial rate of depth reversals. We also measured preferences to see one particular motion direction in front. Unexpectedly, we found that all of our 34 observers had a strong bias to see a particular motion direction in front, and this preferred direction was usually either downward or rightward. In contrast, there was no consistency in seeing the fastest or slowest surface in front. Finally, the preferred motion direction seen in front for one observer was very stable across several days, suggesting that a trace of this arbitrary motion preference is kept in memory.

Keywords: motion transparency, depth perception, ambiguous stimuli, bistable perception, long-term memory

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Introduction

Motion transparency refers to the phenomenological impression of transparency from motion signals. Similarly to stereo and Metelli (or luminance) transparency, motion transparency is associated to a clear depth percept, with one surface that appears to be sliding on top of the other (e.g., Andersen, 1989; Gibson, Gibson, Smith, & Flock, 1959; Kersten, Bülthoff, Schwartz, & Kurtz, 1992). However, contrary to stereo and Metelli transparency, there is no physical signal in motion transparency that can determine the depth ordering without any ambiguity. The segregation of the motion signals into two different surfaces seen simultaneously very often implies that one is seen in front of the other, but from a geometrical point of view, the depth ordering is arbitrary. We are interested here in characterizing the properties of depth assignment in motion transparency.

Past work on motion transparency has primarily focused on the conditions that lead to a transparency percept. For instance, previous studies have determined the minimal direction difference (Braddick, Wishart, & Curran, 2002; Mather & Moulden, 1980; Smith, Curran, & Braddick, 1999) or speed difference (Masson, Mestre, & Stone, 1999; Mestre, Masson, & Stone, 2001) necessary to perceive transparency (which are relatively large compared to non-transparent motion discriminations). Other studies have determined the maximum number of transparent surfaces that can be perceived simultaneously (Andersen, 1989; Edwards & Greenwood, 2005). Motion transparency stimuli are more complex than stimuli containing only a single motion direction and are processed with different efficiencies (Calabro & Vaina, 2006; Suzuki & Watanabe, 2009; Wallace & Mamassian, 2003). Several neural structures are involved in motion transparency, but the cortical area MT/V5 in primates seems critical (Muckli, Singer, Zanella, & Goebel, 2002; Qian & Andersen, 1994). Finally, several models have been proposed to account for the segregation and integration of local motion signals in a bottom-up process (Qian, Andersen, & Adelson, 1994; Snowden & Verstraten, 1999; Zanker, 2005), although higher level influences, such as attention, can affect the perception of transparent motion (Felisberti & Zanker, 2005; Lankheet & Verstraten, 1995; Valdes-Sosa, Cobo, & Pinilla, 2000). While there are numerous previous studies on these topics, the question of apparent depth ordering in motion transparency remains to be addressed.

In contrast to motion transparency that has no unambiguous depth signal, stereo transparency provides a disambiguating depth signal in the form of binocular disparities (e.g., Tsirlin, Allison, & Wilcox, 2008; Wallace & Mamassian, 2004), and only small disparity differences are perceptually averaged (Parker & Yang, 1989; Stevenson, Cormack, Schor, & Tyler, 1992). There are numerous reports describing how binocular and motion signals combine to enrich the perception of transparency (Curran, Hibbard, & Johnston, 2007; Greenwood & Edwards, 2006; Hess, Hutchinson, Ledgeway, & Mansouri, 2007; Hibbard & Bradshaw, 1999). It is tempting to assume that these interactions between motion and stereo transparency occur along a common representation of depth, but this model requires that motion transparency generates a proper depth representation. The purpose of the present study is to better

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understand how this depth representation is constructed. Because depth from motion transparency is ambiguous, we expect that its perception will be bistable. We first investigate the temporal dynamics of the bistability induced by this ambiguous display and measure the implications of adding a cue to easily segment the two surfaces.

Experiment 1: Segmentation cue

Which surface is seen in front in motion transparency is arbitrary. When a motion transparency display is shown for a long time, we can therefore expect an alternation between perceiving one or the other surface in front. In this first experiment, we measure the dynamics of depth assignment. We are also interested in knowing whether the presence of a cue to help segment the two surfaces does affect the dynamics of depth reversals. For this purpose, we decided to use a non-motion cue, namely the color of the dots, as it is readily available on a single frame.

Methods

Participants and apparatus

There were 8 participants, of mean age 23.4 years old. All participants had normal or corrected-to-normal visual acuity and were naive to the purpose of the experiment. Another two participants were excluded because they almost never reported seeing any depth reversal within a stimulus run. Participants were placed in a darkened room at a distance of 57.3 cm from the computer monitor. Their head was restrained by a chin rest and viewing was monocular (one eye covered by an eye patch). The stimuli were generated with the PsychToolBox (Brainard, 1997; Pelli, 1997) and displayed on a CRT 21-inch monitor at a refresh rate of 75 Hz.

Stimuli

The stimuli were random-dot kinematograms (RDKs) depicting two surfaces moving in opposite directions, either to the upper right or to the lower left (Figure 1). These directions were arbitrarily chosen except for a concern to avoid cardinal directions. Both surfaces moved at a constant speed of 2.0 deg/s. The stimuli were presented within a circular aperture of diameter 8.0 deg of visual angle. Each surface was composed of 96 dots, which corresponds to an overall dot density (the proportion of the stimulus area that is occupied by the dots) of 2.0%. Half of the dots were black, the other half white. Stimuli were presented within a run of continuous motion lasting 41 s.

Procedure

The procedure used to measure the dynamics of bistability followed that of Mamassian and Goutcher (2005). The task of the observers was to report which surface they saw in front whenever they heard a beep sound. The first sound was presented on average 1 s after stimulus onset and subsequent sounds occurred every 2 s thereafter. Because the stimulus was presented for a run of 41 s, 20 depth judgments were performed per run. A small

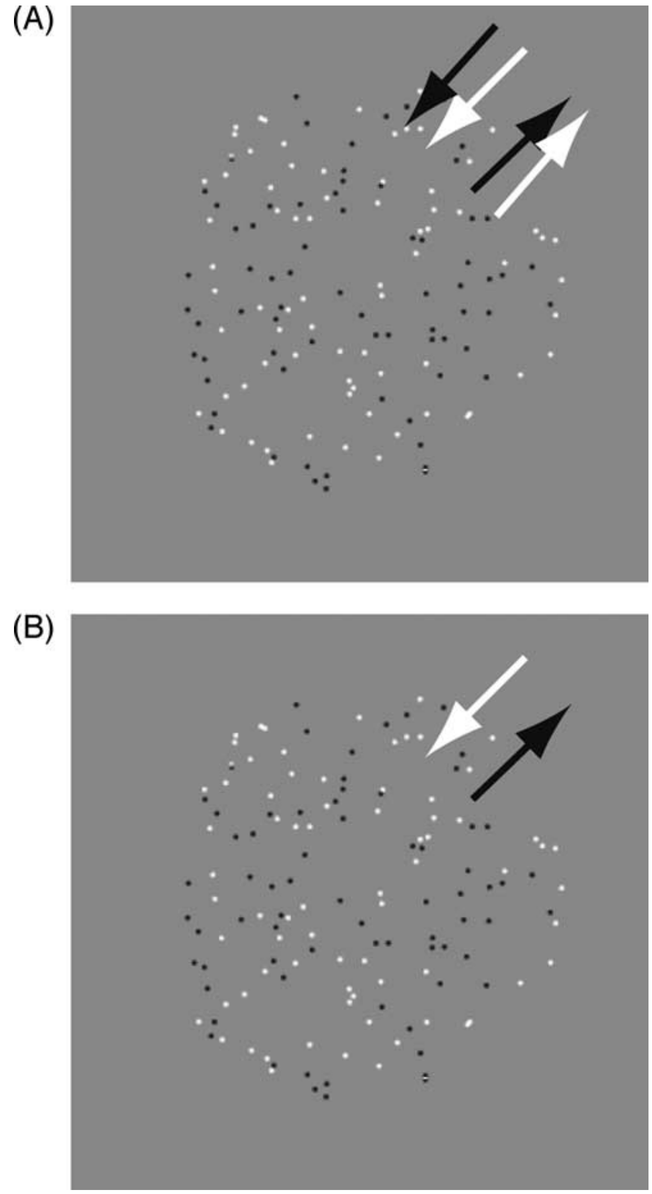


Figure 1. Snapshots of stimuli. (A) No-segmentation condition. Motion transparency was obtained by moving one half of the dots to the upper right and the other half to the lower left. Half of the dots moving in one direction were black and the other half were white, as indicated by the arrows (not displayed). Therefore, the color of the dots could not be used as a segmentation cue. (B) Two-color condition. The stimulus was identical to that shown in (A) except that now all the dots with one color (e.g., black) moved in a single direction (e.g., upper right). The task of the observer was to report the direction of the surface that appeared to be moving in front of the other.

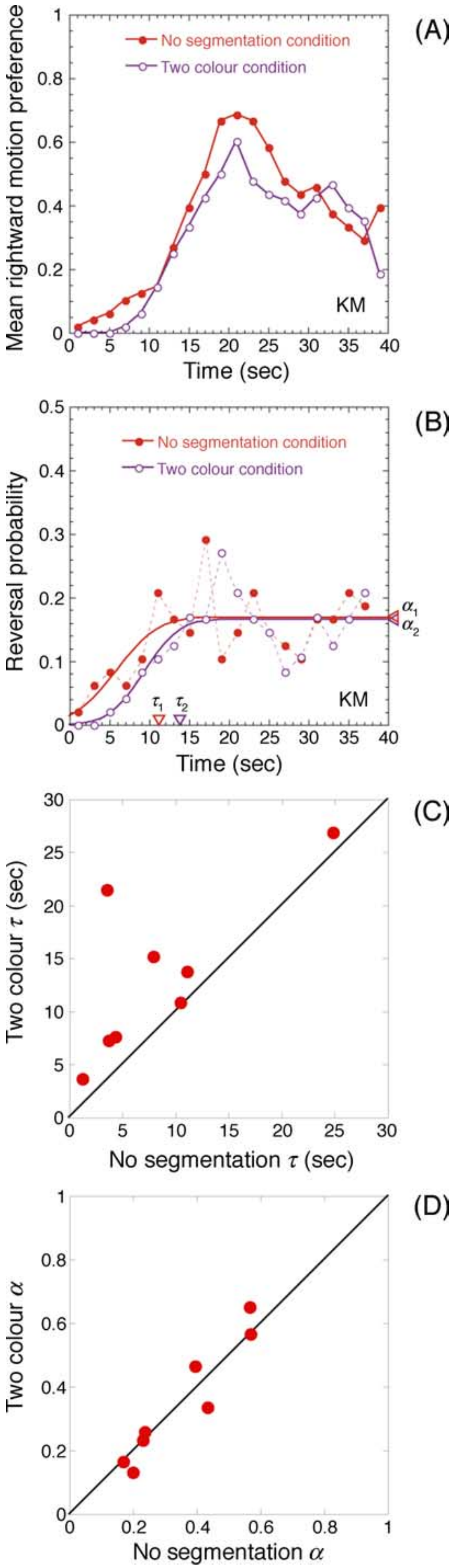


Figure 2. Results of Experiment 1. (A) Mean preference for the surface moving to the right to be perceived in front for one observer (KM). (B) Reversal probability for the same observer as in (A). Note that the two-color condition took longer to reach its stationary regime, but this stationary regime is not different from the one obtained in the no-segmentation condition. (C) Comparison of the time to reach the stationary regimes in both conditions across observers. (D) Comparison of the values of the stationary regime in both conditions across observers.

temporal jitter (within a temporal window of 1 s centered on the mean targeted sample time) was added to reduce the predictability of the next judgment. Observers used one of two keys on the computer keyboard to report the direction of the surface they saw in front at the time of the sound. Because the right arrow key (respectively, left key) was used to report an upper right percept (respectively, lower left), we simply refer to rightward (respectively, leftward) direction judgments in the following.

Two conditions were intermixed. In the *no-segmentation* condition (Figure 1A), half of the black dots moved in one direction and the other half in the opposite direction. The same was true for the white dots. Therefore, each surface was composed of half black and half white dots. In contrast, in the *two-color* condition (Figure 1B), all the black dots moved in one direction and all the white dots moved in the opposite direction. Therefore, in this second condition, the color of the dots was a cue to help segment the stimulus into two surfaces. Which surface color moved to the right rather than left was randomized between runs. Both conditions contained the same number of black and white dots, and the same number of dots moving in each direction, the only difference being whether the dot color was a cue to segment the two surfaces. Each condition was repeated 48 times. The total of 96 runs was presented in random order in 12 blocks of 8 runs and participants were authorized to take short breaks between blocks.

Results

The dynamics of bistability is well characterized by two time-varying probabilities, the transient preference, and the reversal probability (Mamassian & Goutcher, 2005). The former corresponds to the probability to perceive one particular direction of motion (e.g., rightward) in front. The latter corresponds to the probability that the current percept will change at the next evaluation. Each of these probabilities is computed for each of the twenty consecutive judgment times.

Figure 2A shows the transient preference to see the surface moving to the right in front for one observer. This particular observer has a strong initial bias to see the surface that was moving to the left to be the one in front. Other observers showed a range of other biases. We shall come back to this initial preference in the next experiment. After this initial preference, the percept of the observer switched to a preference to see the surface moving to the right as the one in front. In other words, the perception of depth in our motion transparency display was clearly bistable. We analyze further the dynamics of bistability by computing the reversal probability.

Figure 2B shows the reversal probability for the same observer as in Figure 2A. This probability is the likelihood that if the current percept is right direction in front it will switch to left direction in front at the next beep, and reversely if the current percept is left direction in front. The reversal probability shows the characteristic initial rise before reaching a stationary regime (Mamassian & Goutcher, 2005), indicating that the first percepts lasted longer than the subsequent ones. We call τ_1 (respectively, τ_2) the critical time to reach the stationary regime in the no-segmentation condition (respectively, the two-color condition) and α_1 (respectively, α_2) the reversal rate in the stationary regime in the no-segmentation condition (respectively, the two-color condition). We note that for this observer the time to reach the stationary regime is longer in the two-color condition than in the no-segmentation condition (τ_1 = 11.1 s vs. τ_2 = 13.8 s). In contrast, there was no difference in the reversal rate in the stationary regime between the two conditions. These two observations for this particular observer generalize across our population of participants. The time to reach the stationary regime is longer in the two-color condition than in the no-segmentation condition (Figure 2C). In contrast, there was no difference in the reversal rate in the stationary regime between the two conditions (Figure 2D).

Discussion

Depth assignment in motion transparency displays is ambiguous and observers experienced spontaneous reversals when the stimulus was presented for a long time. This bistability for planar motions is similar to the one reported for rotating cylinders (Nawrot & Blake, 1989). In addition, as observed in ambiguous plaid motion (Hupé & Rubin, 2003) and binocular rivalry (Mamassian & Goutcher, 2005), observers tended to hold on their initial percept longer than the subsequent ones. Interestingly, there was a difference in the temporal dynamics of the bistability depending on whether an additional cue was present to segment the two surfaces. When all dots moving in one direction had the same color (the two-color condition), the time to reach the stationary reversal rate was longer than when the colors were distributed across the two surfaces (the no-segmentation condition). In other words, adding a color cue to help segment the two surfaces brought stability to the initial percept. Interestingly, this initial advantage was not present once the stationary regime was reached (both conditions led ultimately to identical reversal rates). Therefore, it appears that the color cue was important only initially to segment the two surfaces but that this cue is neglected once it is judged irrelevant.

In the present experiment, most observers presented strong initial biases to perceive one particular direction of motion in front. We explore more extensively this direction preference in the next experiment.

Experiment 2: Direction bias

In this second experiment, we are interested in measuring the extent to which the direction of motion influences which direction is seen in front when motion transparency is produced by two opposite motion directions. In this experiment and the following ones, we restrict our focus to the initial percept that showed the strongest bias in Experiment 1 (Figure 2A).

Methods

Participants and apparatus

There were 34 participants, of mean age 25.3 years old. All participants had normal or corrected-to-normal visual acuity and were naive to the purpose of the experiment. Another four participants were excluded because they reported always seeing the same colored surface in front (either the black one or the white one, see description in the Stimuli section below). The apparatus was identical to that used in Experiment 1.

Stimuli

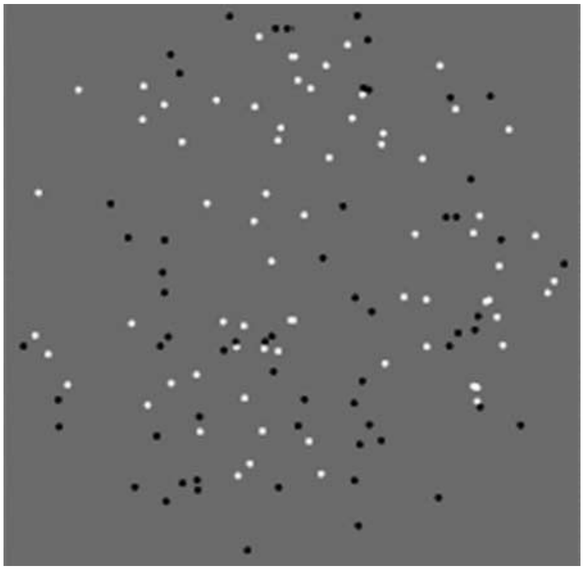
The stimuli were identical to that of the two-color condition of Experiment 1 (Figure 1B). As a reminder, in this condition, one surface is composed exclusively of white dots, and the other exclusively of black dots. The surfaces moved in opposite directions at a constant speed of 2.0 deg/s. Stimuli were presented for 280 ms. Examples of stimuli are shown in Movie 1.

Procedure

The two surfaces always moved in opposite directions, but the direction of motion of the surface composed of black dots was randomly chosen from trial to trial. This direction of motion could take one of 24 values uniformly distributed around the clock, and each orientation was presented 16 times. The 384 trials were divided into 4 blocks and participants were authorized to take short breaks between blocks. The task of the observer was to report the color of the surface that appeared to move in front (black or white). Only their first percept was recorded.

Results

Observers reported whether the surface that appeared in front was composed of black or white dots. Across the



Movie 1. Examples of the 24 directions of motion used in Experiment 2. After each stimulus, participants had to report which surface they saw in front, the one composed of black dots or the one composed of white dots.

38 original participants and across all trials, the mean probability to report the black surface in front was 0.521 (standard deviation of 0.136). While there was no bias overall, four of these 38 observers had a very strong bias (larger than 0.75) in favor of seeing always the same color in front (either black or white). These participants were excluded and the following analyses were carried out on the remaining 34 observers.

The proportion of times the black surface was seen in front is plotted against the direction of motion of the black dots in Figure 3A for two observers. These two observers showed a preference to see the black dots moving in front when they were moving downward. Similarly, they saw the black dots moving behind when they were moving upward, or equivalently, they saw the white dots moving in front when they were moving downward. Overall, these two observers had a strong bias to see the surface moving downward in front.

All observers showed a preference to see one particular direction of motion in front, but this preferred direction varied between observers. In order to characterize the direction bias, as well as the sensitivity with which observers changed their interpretation with motion direction, the data are fitted with a logit model. For each direction of motion of the black dots θ, the probability p to see the black surface in front is characterized by the following logit model:

$$\text{logit}(p) = \ln\left(\frac{p}{1-p}\right) = \gamma - \beta_\theta|\theta - \theta_0|_\pi, \qquad (1)$$

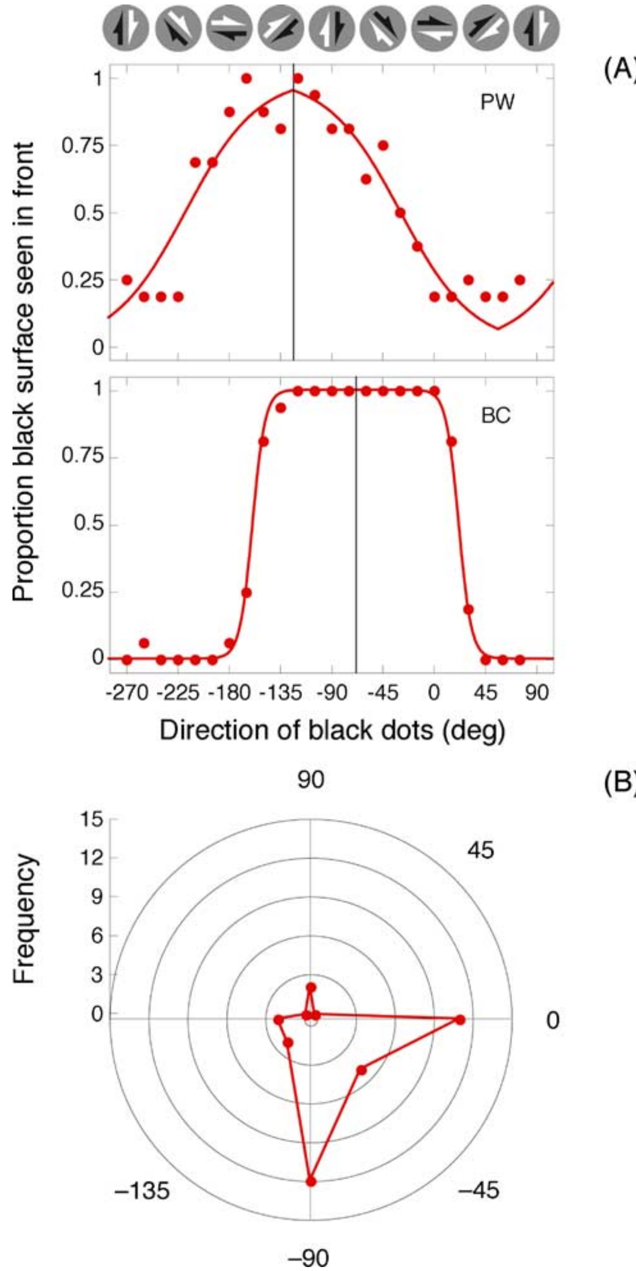


Figure 3. (A) Effect of motion direction on depth assignment in motion transparency. Data for two observers show the proportion of times the surface composed of black dots is seen in front as a function of the direction of the black dots. Motion direction is measured counterclockwise, where 0 is a motion to the right. Observer PW (upper plot) had a strong tendency to see the black surface in front when it was moving downward and slightly to the left. Observer BC (lower plot) had a very strong preference to see the black surface in front when it was moving downward and slightly to the right. The data are fitted by a logit model (see text). (B) Distribution of preferred motion direction for the surface seen in front. The motion direction that was preferentially seen in front was collected for each observer. The plot is the frequency histogram of these preferred directions in polar coordinates. Most observers had a bias to see a surface in front when it was moving either downward or rightward.

where θ_0 is the preferred direction, β_θ represents the strength of the effect of motion direction on the depth percept, and γ is a constant. In this equation, $|\ |_\pi$ stands for the absolute value modulo π, i.e., $|x|_\pi = \text{acos}(\cos(x))$. The parameter β_θ shows how sensitive an observer is for small variations of motion directions (its unit is in rad^{-1} when motion directions are expressed in radians). Some observers, such as BC, are very sensitive to the direction of motion in the sense that rotating the display by just a few degrees makes the black surface perceived always behind to always in front. These observers will display a large value of the parameter β_θ. Other observers, such as PW, will be less affected by the motion direction and will display a smaller value of the parameter β_θ.

In Figure 3A, a vertical black line indicates the value of the parameter θ_0 that represents the motion direction of the black dots that leads to the largest probability to see these black dots in front. Figure 3B shows the distribution of these preferred motion directions leading to a surface seen in front. This distribution is bimodal with a peak for downward motion and the other peak for rightward motion.

Discussion

Depth assignment in motion transparency when two surfaces move in opposite directions is ambiguous. In spite of this ambiguity, all observers presented a preference to see one particular direction of motion. In some cases, this preference was so pronounced that a rotation of the display by 15 degrees led to a reversed depth assignment (see for instance the judgments of observer BC at orientations 15 and 30 degrees in Figure 3A). Preferred directions of motion that were seen in front were idiosyncratic, but there was a clear tendency for these directions to be either downward or rightward.

At present, we do not have any reasonable explanation for such preferences for seeing one motion direction in front. In particular, it is difficult to evoke ecological reasons for the role of motion direction in biasing the percepts of observers. One other aspect of visual motion is speed, and in contrast to direction, the kinetic depth effect offers a prediction about whether the fastest surface should be seen in front. We now turn to the issue of the role of speed in depth assignment.

Experiment 3: Speed bias

The Kinetic Depth Effect (KDE) refers to the motion induced on the retina of an observer who is looking at an object rotating in depth (Wallach & O'Connell, 1953). Because of the laws of perspective projection, parts of the object that are closer to the observer will move faster than those that are farther (Figure 4A). This property holds irrespective of where the observer is looking, as long as she is not tracking one of the object features. Therefore, from KDE, we should expect that the fastest surface should appear in front in a motion transparency display in the case of motion in opposite directions.

Methods

Participants and apparatus

The same observers who took part in Experiment 2 also took part in this new experiment. The apparatus was identical to that of Experiment 1.

Stimuli

The stimuli were identical to that of Experiment 2 with the exception of their speed. One of the two surfaces was assigned a baseline speed of 2.0 deg/s and the other surface was assigned a speed equal to or larger than this baseline value. Stimuli were presented for 280 ms.

Procedure

The speed ratio between the two surfaces varied randomly from trial to trial and could take one of five values between 1 and 4 uniformly distributed on a logarithmic scale. The two surfaces always moved in opposite directions and the motion direction of the black surface was chosen randomly from trial to trial from one of four possible directions (all four main diagonal directions). These two independent variables (speed and direction) were crossed in a full factorial design and each combination was presented 8 times. The 160 trials were divided into 2 blocks and participants were authorized to take a short break between blocks. The task was identical to that of Experiment 2: observers were prompted to report the color of the surface that appeared to move in front (black or white). Only their first percept was recorded.

Results

We first analyze the effect of speed on the assignment of depth to the motion transparency display. Because the four motion directions were just introduced to add more variability to the stimuli, we perform this analysis by pooling the data across motion direction. The proportion of times the fast surface was seen in front was computed for each speed ratio for the same observers as the data shown in Figure 3A (Figure 4B). These data were then fitted with a logit model to estimate the contribution of speed to depth assignment. For each speed ratio κ, the probability p to see the black surface in front is characterized by the following logit model:

$$\text{logit}(p) = \ln\left(\frac{p}{1-p}\right) = \beta_\kappa \ln(\kappa), \quad (2)$$

where β_κ represents the strength of the effect of motion speed on the depth percept. Positive values of the parameter β_κ represent a preference to see the fast surface in front, and negative values represent a preference to see the slow surface in front. Note that the logarithm is used on the right-hand side because the variable of interest is a ratio (as a consequence, β_κ is unitless). Equation 2 can be rewritten to give a simple form for the probability p

$$p = 1/(1 + \kappa^{-\beta_\kappa}). \quad (3)$$

For the two observers displayed in Figure 4B, one saw consistently the slow surface in front and the other was not at all influenced by speed (a parameter β_κ close to zero). Overall, most observers showed little effect of speed (Figure 4C). If anything, there is a small bias to see the slow surface in front.

We take the absolute value of the parameter β_κ as a measure of the speed bias strength: the larger the value, the stronger the effect of speed. For instance, in Figure 4B, observer PW was more influenced by speed than observer BC and this is well captured by the magnitude of β_κ. We can also perform a similar analysis with the data collected in the previous experiment. The strength with which motion direction determined which surface was seen in front is characterized by the magnitude of the parameter β_θ. When these two parameters are compared, we observe a trade-off (Figure 5). There is a significant negative correlation between the directional bias and the speed bias strengths (Pearson's correlation R = 0.680). In other words, those observers who were very much influenced by the stimulus speed were less influenced by its direction and conversely.

Discussion

Contrary to our prediction that the fastest surface should be seen in front in a motion transparency display, most observers were not influenced by speed to assign depth in these ambiguous stimuli. Moreover, among those who were influenced by speed, the number of observers who

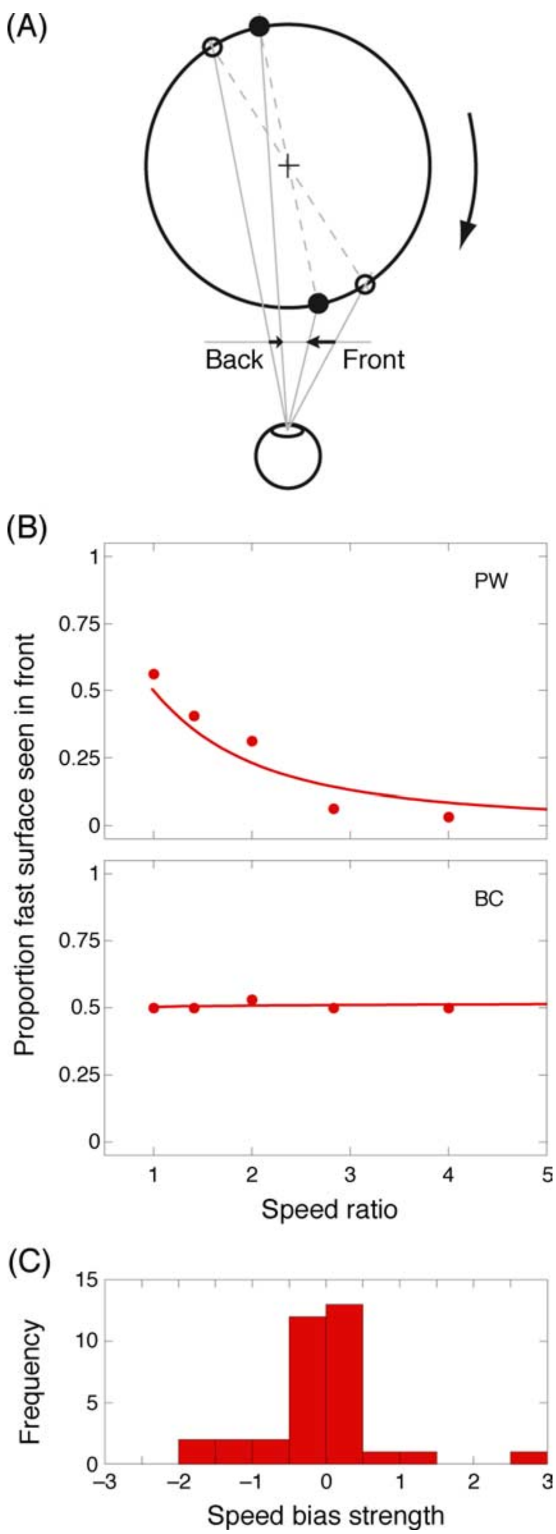


Figure 4. (A) Geometry of the Kinetic Depth Effect for a rotating transparent cylinder. Features in front of the cylinder have a faster retinal motion than those in the back. (B) Effect of speed on depth assignment in motion transparency. Data for two observers (same as in Figure 3A) show the proportion of times the fast surface is seen in front as a function of the speed ratio between the two surfaces. Observer PW (upper plot) saw the slow surface in front, and more so as the speed difference between the two surfaces increases. Observer BC (lower plot) was not influenced at all by the speed difference. The data are fitted by a logit model (see text). (C) Distribution of fast surface seen in front. The plot is the frequency histogram of the β_κ parameter of the logit model that represents the strength of the speed bias. Positive values indicate a preference to see fast surfaces in front; negative values indicate slow surfaces in front. Most observers were not affected by the speed difference between the surfaces, as illustrated by the peak of the histogram at zero.

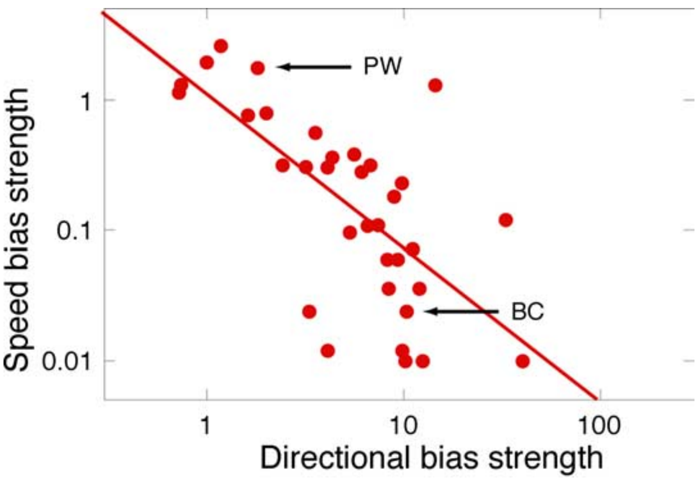


Figure 5. Correlation between the speed bias and the motion bias strengths. The speed bias strength represents how strongly the speed difference between the two surfaces could affect which surface was seen in front. The motion bias strength represents how sensitive to the motion direction the observer was to assign one surface in front. These two measures are negatively correlated. Note that the two bias strengths do not have the same units (see Equations 1 and 2). Each point represents an observer (observers PW and BC from Figures 3 and 4 are highlighted). The line is the best linear regression.

saw the fast surface in front was smaller than the number of those who saw the slow in front.

There is a trade-off between the strength of the directional bias and the strength of the speed bias. It may be that, when faced with a very ambiguous stimulus, participants attempted to use any cue hypothesized to be relevant. As a consequence, some participants attended specifically to the direction of motion and others to the relative speed between the two sets of dots. Alternatively, this result could indicate the involvement of a neural structure that codes both depth and motion properties (direction and speed). Such cells have been found in cortical area MT/V5 when depth is depicted by binocular disparities (Bradley, Chang, & Andersen, 1998; Bradley, Qian, & Andersen, 1995; Rokers, Cormack, & Huk, 2009). It will be interesting to explore further the neural mechanisms underlying the directional and speed biases in the future.

In contrast to speed, motion direction produces clear biases for all observers. We are exploring the robustness of these biases in the last experiment.

Experiment 4: Stability of the direction bias

In the second experiment, we encountered an unexpected effect of the motion direction on the assignment of depth ordering in motion transparent displays. We found that not only all observers have a preferred direction of motion that they see in front but this preferred direction tend to be either downward or rightward. We are now interested in knowing whether the preferred motion direction to see one surface in front is robust in time.

Methods

Participants and apparatus

We asked 10 observers to take part in this new experiment (mean age 24.4 years old). All observers were naive to the purpose of the experiment, but eight of them did participate in the previous two experiments. The apparatus was identical to that of Experiment 1.

Stimuli and procedure

The stimuli were identical to that of Experiment 2. The procedure was identical to that of Experiment 2, except that observers were tested over 10 sessions, one per day of the week for 2 weeks (excluding the weekend), instead of just once.

Results

The preferred motion direction seen in front is plotted separately for the different observers in Figure 6. Apart from idiosyncrasies across observers in terms of their preferred direction, each observer was highly stable in keeping the same preferred direction across 2 weeks of testing. The standard deviation of preferred directions across the ten sessions averaged 7.23 degrees across observers.

Discussion

In the second experiment, we found a surprising effect of motion direction on the assignment of depth order in motion transparency displays. In this last experiment, we have established that the preferred motion direction is not random within an observer but instead is very stable across 2 weeks.

General discussion

In motion transparency, one surface is very often seen on top of another, but there are no unambiguous signals to determine which surface should be in front. Therefore, it is not surprising that when a motion transparency stimulus

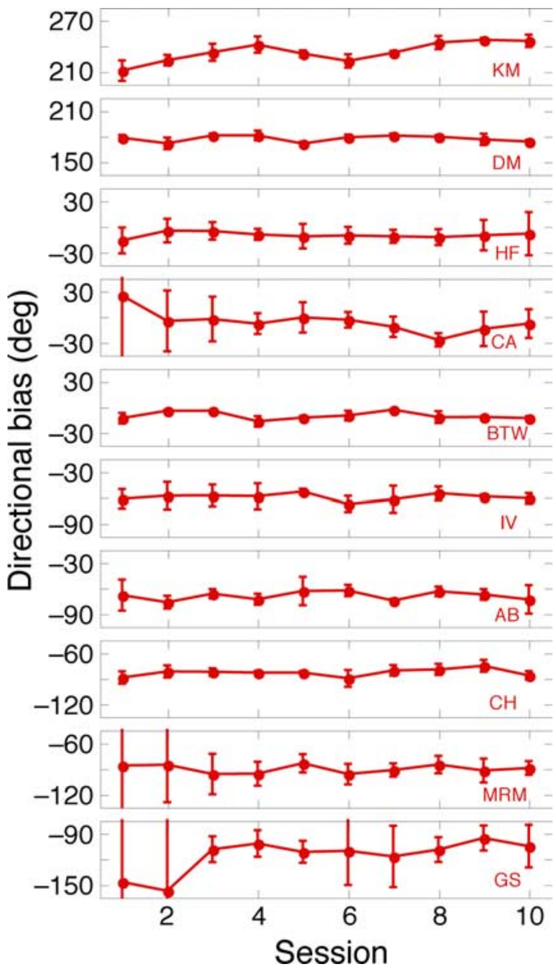


Figure 6. Stability of the preferred motion direction for the surface seen in front. Preferred motion directions for a surface seen in front were measured in one session per day, every day for 2 weeks (except the weekend). Data are presented for 10 observers. Preferred motion directions were extremely stable across days. Error bars represent the inverse of the strength of the directional bias as inferred from the directional logit model in the text (each side of the bar shows $100/\beta_\theta$).

is seen for a long time, perception is bistable in the sense that spontaneous depth reversals repeatedly exchange the front and the back surfaces. When the moving surfaces have different colors, the initial percept is longer than if no-segmentation cue is available.

We tested the hypothesis that when there is a speed difference between the two surfaces, the fastest should be seen in front if perception follows the geometry of the kinetic depth effect. We found no evidence for this speed hypothesis for the initial percept. Alternatively, it has been suggested that eye movements, specifically the involuntary optokinetic response, may influence perceived depth ordering for motion parallax stimuli, such that the motion in the same direction as the eye movement is perceived as being nearer (Nawrot, 2003). Direction of optokinetic eye movements has been correlated with perception of depth in transparent displays of opposite motions (Watanabe, 1999), and in motion parallax displays, reflexive eye movements have been shown to follow the slowest velocity present in the stimulus, but only after depth has been detected (Mestre & Masson, 1997). In our study, if observer's involuntary eye movements were consistently in the direction of the slow surface, and this did determine perceived depth ordering, this could account for the results of speed for only a small fraction of our participants.

We also tested whether the orientation of the stimulus could play a role when the two surfaces moved in opposite directions and found clear preferences for one motion direction to be in front. These preferred directions of motion varied from one observer to the next but tended to be either downward or to the right. In addition, even though each observer has a bias that is idiosyncratic, this bias is extremely stable over time.

There are other reports of anisotropies in perceived motion direction from ambiguous displays. In particular, Morikawa and McBeath (1992) found a leftward bias in the interpretation of ambiguous horizontal apparent motion. According to the authors, this leftward bias is possibly related to the direction of reading, since when a text is scanned from left to right, it produces a leftward motion on the retina. This bias cannot by itself explain the directional biases reported here. Notwithstanding the fact that half of our observers displayed a downward bias rather than a horizontal one, it is not clear why leftward bias in apparent motion perception translates to a rightward bias to perceive this surface in front in a transparent display.

The long-lasting bias for a particular direction to be seen in front represents the storage of some sensory information, and as such can be seen as an instance of perceptual memory (Magnussen & Greenlee, 1999). Memory has been recently found to play an important role in bistable perception. Most notably, when an ambiguous display is regularly interrupted, observers tend to interpret the display in the same way as it was before the interruption (Brascamp, Pearson, Blake, & van den Berg, 2009; Leopold, Wilke, Maier, & Logothetis, 2002). With the motion quartet stimulus, observers tend to see the same interpretation on consecutive trials, but they are also more likely to change their interpretation if alternation completes a temporal pattern (Maloney, Dal Martello, Sahm, & Spillmann, 2005). In perceptual grouping, negative contingencies have been found between the interpretation of an ambiguous display in one trial and the interpretation of a similar display in the next trial (Gepshtein & Kubovy, 2005). However, these effects occur over a short time scale (in the sub-second to the second range) whereas the preference for one particular direction in our experiments lasts days. This is a surprising result because our observers went on carrying their usual life in between sessions and supposedly encountered situations where they had to make perceptual decisions on complex motion stimulations. A similar long-lasting effect in the interpretation of ambiguous displays has been found after training observers to see a Necker cube rotate in one particular direction (Haijaing, Saunders, Stone, & Backus, 2006; Harrison & Backus, 2010; van Dam & Ernst, 2010). In our experiments, it is as if observers kept in memory a prior for one motion direction to be in front that might have been assigned in a rather arbitrary manner but that remains extremely stable across time.

There are only a few other reports of long-term retentions of visual properties that are acquired implicitly. One such example is the McCollough (1965) effect, where a contingent aftereffect between two visual attributes can last for weeks (Jones & Holding, 1975). Another example is the memory of a response criterion in spatial frequency discrimination (Lages & Paul, 2006). These effects are all examples of long-term memory of encoding of past perceptual decisions and ambiguous displays such as the one used here might turn out to be a useful tool to study them in the future.

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