Motion transparency: Depth ordering and smooth pursuit eye movements

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When two overlapping, transparent surfaces move in different directions, there is ambiguity with respect to the depth ordering of the surfaces. Little is known about the surface features that are used to resolve this ambiguity. Here, we investigated the influence of different surface features on the perceived depth order and the direction of smooth pursuit eye movements. Surfaces containing more dots, moving opposite to an adapted direction, moving at a slower speed, or moving in the same direction as the eyes were more likely to be seen in the back. Smooth pursuit eye movements showed an initial preference for surfaces containing more dots, moving in a non-adapted direction, moving at a faster speed, and being composed of larger dots. After 300 to 500 ms, smooth pursuit eye movements adjusted to perception and followed the surface whose direction had to be indicated. The differences between perceived depth order and initial pursuit preferences and the slow adjustment of pursuit indicate that perceived depth order is not determined solely by the eye movements. The common effect of dot number and motion adaptation suggests that global motion strength can induce a bias to perceive the stronger motion in the back.

Keywords: motion transparency depth rivalry, perceptual rivalry, bistability, smooth pursuit eye movements, motion coherence, transparent motion, random-dot kinematogram, perceived depth, motion adaptation

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Introduction

Perception can be considered as an active process in which the brain is trying to make sense out of the available sensory input (von Helmholtz, 1894). This process can be observed in particular when the sensory input is ambiguous (for reviews, see Leopold & Logothetis, 1999; Parker & Krug, 2003; Sterzer, Kleinschmidt, & Rees, 2009). Well-known examples are bistable figures such as the Necker (1832) cube, where different interpretations of the same retinal stimulus are possible, and binocular rivalry (for a review, see Blake & Logothetis, 2002), where different images are presented to the two eyes. In case of motion transparency (for a review, see Snowden & Verstraten, 1999), when two transparent surfaces move in different directions or at different speeds, there is ambiguity with respect to the depth ordering of the surfaces. This has been recently termed motion transparency depth rivalry (Chopin & Mamassian, 2011).

While there is extensive research on factors influencing dominance in binocular rivalry, little is known about factors influencing motion transparency depth rivalry. The influence of surface features on depth ordering is important from an ecological perspective because there are a variety of features that change with depth under natural conditions. Among these features are, for instance, speed and spatial frequency of the surface textures. Surface features are also interesting from a neurophysiological perspective: If there are surface differences, the visual system not only has to represent two different motion vectors at the same position but also two different surface features. Moreover, the representation of these features has to be linked to the corresponding motion vector, to achieve a coherent percept.

So far, there is no clear picture which features effectively determine depth order. One study investigated the influence of surface features, like wavelength, duty cycle, and speed of moving gratings on depth ordering during prolonged exposure (Moreno-Bote, Shpiro, Rinzel, & Rubin, 2008). The results showed that gratings with higher spatial frequencies, smaller duty cycles, and faster speeds appear more often in the back. Another study did not find any effect of speed but found surprisingly robust preferences to see upward or leftward motion in the back (Mamassian & Wallace, 2010). These studies used either a fixation spot (Moreno-Bote et al., 2008) or did not measure eye movements (Mamassian & Wallace, 2010).

However, transparent motion can trigger smooth eye movements, and thus, motion transparency depth rivalry is a particularly interesting case of perceptual ambiguity (Maruyama, Kobayashi, Katsura, & Kuriki, 2003; Mestre & Masson, 1997; Niemann, Ilg, & Hoffmann, 1994; Schütz, Braun, Movshon, & Gegenfurtner, 2010; Watanabe, 1999). Smooth eye movements are important in this context because of two reasons: first, they have been shown to disambiguate the retinal input for depth perception, and second, the neural networks responsible for motion and depth perception and for the control of smooth pursuit eye movements are overlapping.

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Smooth pursuit eye movements play a crucial role in motion parallax (Rogers & Graham, 1979). Motion parallax is an informative depth cue if an observer is translating in a scene. As a consequence of the translational motion, close objects move faster on the retina than far objects. However, usually observers fixate a stationary object under these conditions, so that the eyes move in a direction opposite to the translation. In this case, the retinal speed alone is only informative about the absolute distance in depth relative to fixation, i.e., objects close to fixation move slower on the retina than objects far away from fixation. Objects in front or behind the fixation move in opposite directions on the retina, but the assignment of direction to depth sign is ambiguous. There is behavioral (Naji & Freeman, 2004; Nawrot & Joyce, 2006) and physiological (Nadler, Angelaki, & DeAngelis, 2008; Nadler, Nawrot, Angelaki, & DeAngelis, 2009) evidence that the extraretinal signal of smooth pursuit eye movements is used to disambiguate the retinal input. Another example for the close relationship between motion and depth is the kinetic depth effect or structure from motion (Wallach & O'Connell, 1953), where depth or three-dimensional form can be extracted from two-dimensional projections of three-dimensional objects, if the objects are rotating. In contrast to motion parallax, the observer is typically stationary and the object is rotating. Although both motion parallax and kinetic depth emphasize the close relationship between motion and depth, there are some important differences to motion transparency. Motion parallax typically involves self-motion of an observer, and in the kinetic depth effect, the different layers of motion belong to one object.

There is considerable overlap between the neural networks for motion perception, smooth pursuit eye movements, and depth perception. Area MT contains direction-selective neurons and is a key structure for processing of motion for perception (Britten, Shadlen, Newsome, & Movshon, 1992; Newsome, Wurtz, Dursteler, & Mikami, 1985; Salzman, Murasugi, Britten, & Newsome, 1992) as well as smooth pursuit eye movements (Dursteler, Wurtz, & Newsome, 1987; Lisberger & Movshon, 1999). More recent evidence shows that MT is also involved in processing of depth, because it contains disparity-selective neurons (Bradley, Chang, & Andersen, 1998; Bradley, Qian, & Andersen, 1995) and neurons that are selective for depth from motion parallax (Nadler et al., 2008, 2009). MT is also involved in the perceptual decision process for ambiguous structure-from-motion stimuli (Bradley et al., 1998; Brouwer & van Ee, 2007; Dodd, Krug, Cumming, & Parker, 2001). If area MT not only controls motion analysis for smooth pursuit but also the depth ordering in motion transparency, smooth pursuit eye movement choices and perceived depth order should depend on the same surface properties. Since the initiation of smooth pursuit closely resembles early processing of visual motion (Lisberger & Movshon, 1999; Pack & Born, 2001; for reviews, see Schütz, Braun, Gegenfurtner, 2011; Spering & Montagnini, 2011), it is possible to measure the influence of low-level motion factors and to compare that with the perceptual depth ordering.

Here, we investigated the influence of surface differences in transparent motion on the resolution of the ambiguous depth ordering and on smooth pursuit eye movements. Investigating several surface features is important for two reasons: First, it allows to determine which features the visual system associates with depth order. Second, it allows to investigate potential covariations between depth order and smooth eye movement choices.

Methods

Subjects

The author and nine naive observers participated in these experiments (five males and five females, age between 22 and 31). The naive observers were students of the Justus-Liebig-University Giessen and were paid for participation. Four of the naive observers had previous experience with eye movement experiments. Experiments were in accordance with the principles of the Declaration of Helsinki and approved by the local ethics committee LEK FB06 at the University Giessen (Proposal Number 2009-0008). All experiments were performed by ten observers, except Experiment 6, which was performed by seven observers.

Equipment

Observers were seated in a dark room facing a 21-inch SONY GDM-F520 CRT monitor driven by an Nvidia Quadro NVS 290 graphics board with a refresh rate of 100 Hz non-interlaced. At a viewing distance of 47 cm, the active screen area subtended 45 degrees of visual angle (deg) in the horizontal direction and 36 deg vertical on the subject's retina. With a spatial resolution of 1280 × 1024 pixels, this results in 28 pixels/deg. The observers' head was stabilized by chin and forehead rests, and the display was viewed binocularly. Eye position signals of the right eye were recorded with a video-based eye tracker (EyeLink 1000; SR Research, Osgoode, Ontario, Canada) and were sampled at 1000 Hz. Stimulus display and data collection were controlled by a PC.

Visual stimuli

All stimuli were presented on a black background with a luminance of 0.04 cd/m^2. The random-dot kinematograms appeared within a circular aperture of 10-deg radius, except for Experiment 4, where the aperture size was varied to manipulate the dot density. Individual dots were displayed in white (87 cd/m^2) and had a size of 0.14 × 0.14 deg, except for Experiment 5, where the dot size was manipulated as independent variable. The overall dot density was 2 dots/deg^2, except for Experiment 4, where the dot density was varied as independent variable. The dots had a lifetime of 200 ms, and at the end of their lifetime, they were positioned at a random position in the aperture. The motion speed was 10 deg/s, except for Experiment 3, where speed was manipulated as independent variable. The dots were distributed equally to two surfaces, except for Experiments 1, 2, and 6, where the relative dot number was manipulated as independent variable. The motion directions of the two surfaces were separated by 45 angular degrees (°), except for Experiment 2, where the separation was 90°. With 45° separation, motion could occur in the four cardinal and four oblique directions, and with 90° separation, motion could occur only in cardinal directions. The fixation target in Experiment 2 and the eye movement target in Experiment 6 were a red bull's-eye with an outer radius of 0.3 deg and an inner radius of 0.15 deg.

Experimental procedure

At the beginning of each trial, a white bull's-eye with an outer radius of 0.3 deg and an inner radius of 0.075 deg appeared at the screen center. The observers had to fixate the bull's-eye and press a button to start the trial, at which time the EyeLink 1000 System performed a fixation check. If the fixation check succeeded, the initial bull's-eye disappeared and the random-dot kinematogram appeared. Motion started as soon as the dots appeared. The random-dot kinematogram was presented for 1000 ms. At the end of the trial, observers had to indicate which motion direction they perceived further away, except for separate sessions in Experiment 1, where they had to indicate the motion direction they perceived closer (Figure 1A). In Experiments 1 to 5, they responded by a key press on the numeric keypad. In Experiment 6, observers saw after each trial a red line ranging from the screen center to the edge of the aperture. By pressing one button, the observers could switch the orientation of the line between the two motion directions of the surfaces back and forth. By pressing another button, they confirmed their selection. The initial orientation of the line was randomized (Figure 1B). Due to the short presentation duration and the

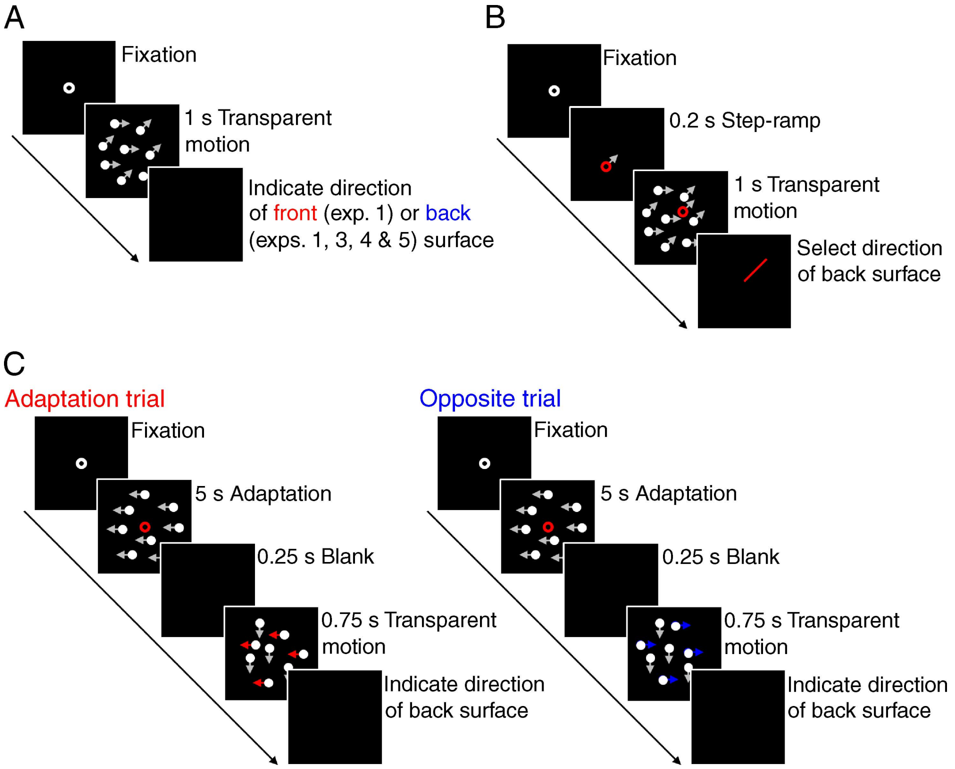

Figure 1. Experimental paradigms. (A) Schematic trial sequence in Experiments 1, 3, 4, and 5. Front and back judgments in Experiment 1 were collected in separate sessions. In Experiments 3, 4, and 5, only back judgments were collected. (B) Schematic trial sequence in Experiment 6. Observers were instructed to pursue the red bull's-eye. (C) Schematic trial sequence of an adaptation and an opposite trial in Experiment 2. Adaptation and opposite trials were presented interleaved; the adaptation direction was blocked. (A–C) The arrows indicate the motion direction of the dots.

response collection at the end of the trial, this experimental procedure captures only the initial depth ordering and not the occurrence of perceptual switches.

Eye movement analysis

Eye velocity signals were obtained by digital differentiation of eye position signals over time. The eye position and velocity signals were filtered by a Butterworth filter with cutoff frequencies of 30 and 20 Hz, respectively. Saccade onset and offsets were determined with the EyeLink saccade algorithm. This algorithm uses a velocity threshold of 22 deg/s to which the average velocity over the last 40 ms is added and an acceleration threshold of 3,800 deg/s^2. Saccades were removed from the velocity traces by linear interpolation. For each trace, the angular direction of the eye velocity was calculated in 100-ms-wide time intervals centered on 0 to 800 ms (700 ms in Experiment 2) after transparent motion onset. Binary eye movement decisions were classified according to which surface direction was closer to the eye movement direction. This procedure allowed a convenient comparison with perceptual depth judgments, which were also given as proportions. We concentrated especially on the time interval 200 ms after motion onset, because it should provide an estimation of initial, bottom-up driven eye movement choices.

Experiments

We performed six different experiments (Table 1), in which we tried to introduce depth biases by varying different surface parameters. In Experiment 1, the distribution of dots to the two surfaces, i.e., the dot number in each surface, was varied in ratios of 1, 2, 3, and 4. In separate sessions, observers had to indicate the direction of the surface in the front or in the back. In Experiment 2 (Figure 1C), observers viewed a single surface, the adaptor, moving left- or rightward for 5 s. The motion direction of the adaptor was blocked. During the adaptation, a red bull's-eye was present as a fixation target. After the adaptation, the screen was black for 250 ms, followed by a transparent motion display for 750 ms. One of the surfaces always moved vertically, i.e., orthogonal to the adaptor. The other surface moved either in the adapted direction or in the opposite direction. The distribution of dots to the vertically and horizontally moving surfaces was varied in ratios of 0.25, 1, and 4. In Experiment 3, the speed of the surfaces was varied in ratios of 1, 2, 3, and 4. The average speed of the two surfaces was kept constant at 10 deg/s. In Experiment 4, the dot density was varied in ratios of 1, 2, 3, and 4, by varying the aperture size and keeping the dot number constant. In Experiment 5, the dot area was varied in ratios of 0.11, 0.44, 1.0, 1.78, and 2.78. In Experiment 6 (Figure 1B), the observers were instructed to follow a red bull's-eye, which moved in the same direction as one of the surfaces. To facilitate smooth tracking, the bull's-eye initially made a 2-deg step in the direction opposite to its motion direction (Rashbass, 1961) and moved for 200 ms, before the transparent surfaces appeared. The distribution of dots to the two surfaces was varied in ratios of 0.25, 1, and 4.

Statistical analysis

Based on the perceptual judgments and the eye movement directions, the proportion of perceptual and eye movement choices was calculated separately for each level of the manipulated surface differences. Average proportions and confidence intervals across observers were calculated in logit space. Since there were no hypotheses about the direction of effects, all statistical tests were calculated two-tailed.

To account for the effects of surface differences (x), e.g., dot number ratio in Experiment 1, on the proportion of depth judgments or eye movement decisions (y), the following logit model (Mamassian & Wallace, 2010) was fitted to the data:

$$y = 1/(1 + x^{-s}). \tag{1}$$

The only free parameter s, the surface index, can range from negative infinity to infinity and is zero if the surface difference has no influence on perception or eye

Experiment	Manipulation	Task
Experiment 1	Surface dot number ratio (1, 2, 3, 4)	Back and front judgments
Experiment 2	Motion adaptation and surface dot number ratio (0.25, 1.0, 4.0)	Back judgments
Experiment 3	Surface speed ratio (1, 2, 3, 4)	Back judgments
Experiment 4	Surface density ratio (1, 2, 3, 4)	Back judgments
Experiment 5	Dot size ratio (0.11, 0.44, 1.0, 1.78, 2.78)	Back judgments
Experiment 6	Eye movements and surface dot number ratio (0.25, 1.0, 4.0)	Back judgments

Table 1. Overview of experiments.

movements. Hence, the surface index quantifies the influence of the surface difference, e.g., the dot number ratio or speed ratio on the perceived depth ordering or on smooth pursuit eye movement choices. This model was used in all experiments, except for Experiments 2 and 6.

To account for the effects of adaptation in Experiment 2, a second free parameter (a), the adaptation index, was added. It was allowed to differ between the adaptation and opposite directions. The surface index (s) was kept identical for the adaptation and opposite directions:

$$y_{\text{adapt}} = 1/(1 + (x/e^{a_{\text{adapt}}})^{-s}), \tag{2}$$

$$y_{\text{opposite}} = 1/(1 + (x/e^{a_{\text{opposite}}})^{-s}). \tag{3}$$

The adaptation index is zero if there is no influence of adaptation, negative for a leftward shift (more back choices) of the function, and positive for a rightward shift (fewer back choices) of the function. The adaptation index moves the function horizontally, along the independent variable, here dot number ratio. Hence, the model assumes that adaptation influences perceived depth order, by modulating the effect of dot number or by modulating a third, common factor of adaptation and dot number.

To account for the effects of the eye movement instruction in Experiment 6, the logit model from Equation 1 was extended by an additive parameter (c), which shifts the function along the vertical axis:

$$y = 1/(1 + x^{-s}) + c. \tag{4}$$

The additive shift index ranges from −0.5 to 0.5, with positive numbers meaning that the surface moving in the same direction as the eye movement target is more often seen in the back. This additive shift index is independent of the surface index, in contrast to the adaptation index used for the adaptation effect in Experiment 2.

We also wanted to investigate directional biases of depth order judgments (Mamassian & Wallace, 2010) and smooth pursuit eye movements. To estimate how often one direction was preferred over another direction and to compare that with the bias induced by the surface difference, the direction deviation (r) was calculated as the root-mean-squared difference of the proportion of choices (y) to 0.5, summed over all pairs of surface directions:

$$r = \sqrt{\sum\nolimits_{i=1}^{n} (y_i - 0.5)^2 / n}. \tag{5}$$

This direction deviation is 0 if there are no systematic direction influences or 0.5 if perception or pursuit are completely determined by motion direction. The direction deviation was calculated only for conditions with no surface differences.

Results

Experiment 1: Dot number

In the first experiment, we varied the distribution of dots to the two motion surfaces in ratios from 1 to 4. Observers had either to indicate the direction of the surface in the back or the surface in the front in separate sessions. Perceptually, the direction of the surface with more dots was reported more often in the back judgment sessions and less often in the front judgment sessions (Figure 2A). Hence, the surface with more dots was seen in the back. This was not a mere response bias, because in this case both back and front judgments would have to be biased toward the surface containing more dots. The eye movements, however, initially followed more often the surface with more dots, irrespective of the perceptual task (Figure 2B). Toward the end of the trial, eye movements became more similar to perception (Figure 2C).

A logit model was used to estimate the bias induced by the relative number of dots in the two surfaces (Equation 1). The surface index ranges from negative infinity to infinity, with extreme values indicating strong surface biases and zero indicating no surface bias. The perceptual surface index for back judgments was, on average, 0.45 (±0.48) and significantly larger than zero ($t(9) = 2.97$, $P = 0.02$). For front judgments, it was, on average, −0.30 (±0.38) and significantly smaller than zero ($t(9) = -2.47$, $P = 0.04$). This shows that the surface with more dots was seen more often in the back and the surface with less dots more often in the front. There was a significant negative correlation between the surface indices in back and front judgments ($r = -0.68$, $P = 0.03$). Hence, observers with a strong bias in back judgments also had a strong bias in front judgments (Figure 2D). These results show that front and back judgments were, in general, complementary. Because of that, we only tested back judgments in the following experiments.

Pursuit 200 ms after motion onset followed more often the surface with more dots, because surface indices were significantly larger than zero for both conditions (back: 1.04 (±0.23), $t(9) = 14.26$, $P < 0.01$; front: 1.08 (±0.41), $t(9) = 8.35$, $P < 0.01$). However, the pursuit behavior changed over time, becoming more similar to perception (Figure 2E): The surface index reached its maximum 200 ms after motion onset and decreased afterward. In both conditions, it decreased to a level comparable to the perceptual surface index. Since the late pursuit preferences depended on the perceptual task and resembled the perceptual preferences, it is most likely that pursuit was

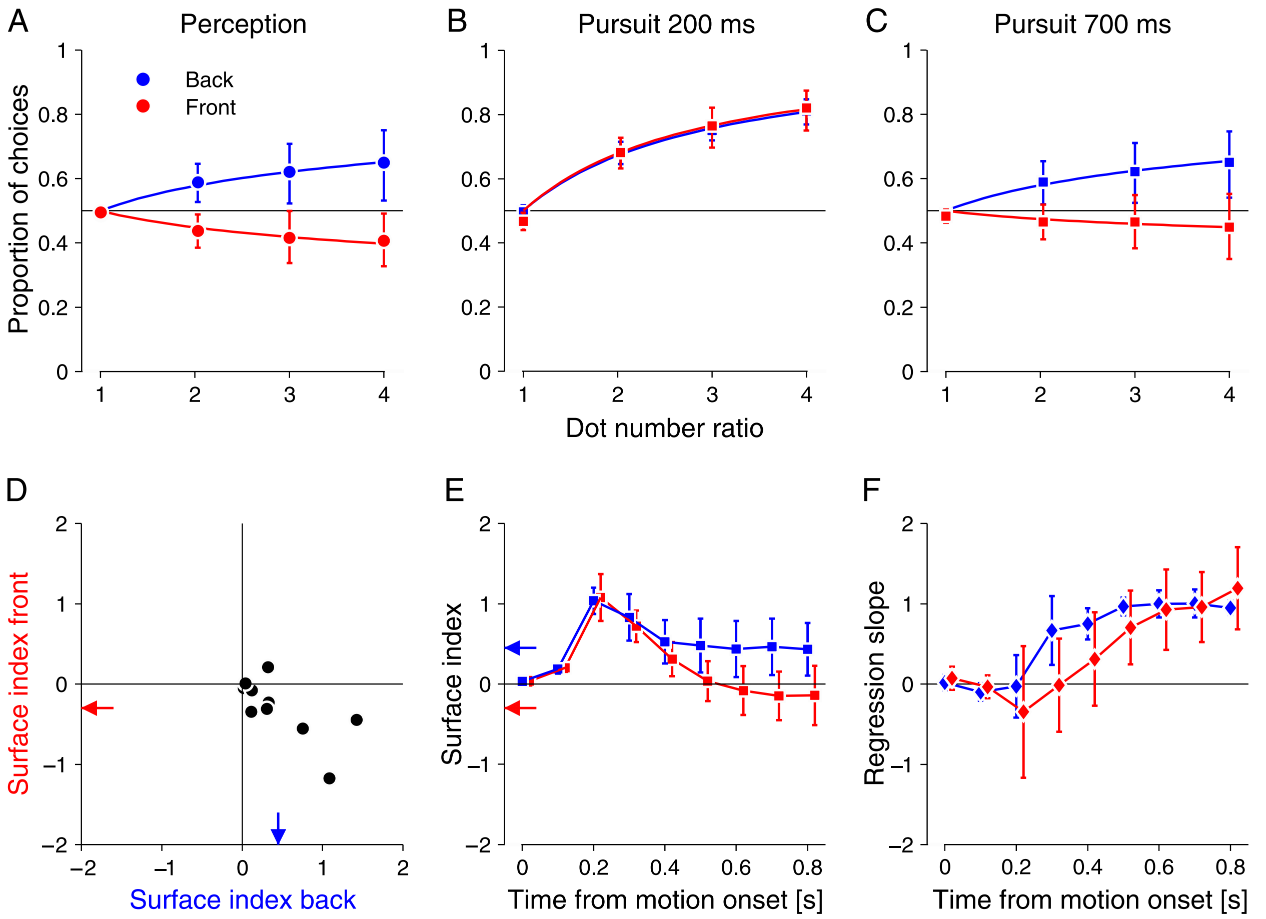

Figure 2. Experiment 1, influence of dot number. (A–C) Average proportion of choices across observers. The lines are obtained by fitting the logit model from Equation 1. (A) Proportion of back and front judgments. (B, C) Proportion of pursuit choices 200 and 700 ms after motion onset. (D) Perceptual surface index for front judgments over surface index for back judgments. (E) Average pursuit surface index over time. (D, E) The blue and red arrows represent the average perceptual surface indices for back and front conditions, respectively. (F) Slope of regression of pursuit surface index on perceptual surface index. (E, F) The values for front and back judgments are horizontally offset to improve the visibility. (A–F) Blue indicates the condition in which observers reported the direction of the back surface; red indicates the condition in which observers reported the direction of the front surface. Perception is indicated by circles; pursuit is indicated by squares. Error bars indicate 95% confidence intervals.

influenced by perception and not vice versa. To analyze the time course of the influence of perception on pursuit more closely, we calculated a linear regression of pursuit on perception for the surface indices across all observers. If the perceptual depth ordering affects eye movement choices, the regression slopes should be different from zero. Regression slopes were significantly larger than zero after 300 ms in the back condition and after 500 ms in the front condition (Figure 2F). This indicates that pursuit is initially only influenced by low-level properties of the display and only later affected by the perceptual task and/or attention (Watanabe, 1999).

Recently, it has been shown that observers have biases to see certain directions in front and more importantly that these directional biases constrain the possible influence of speed differences on depth ordering (Mamassian & Wallace, 2010). In that study, the magnitude of directional biases was negatively correlated with the influence of speed, so that observers with strong directional biases showed little effect of speed. We can estimate the directional biases of our observers in the condition where the dots were equally distributed to the two surfaces, i.e., dot number ratio is unity. In this condition, it was calculated how often one of two directions was chosen over the other (Figure 3A). For some of the direction pairs, the values were clearly smaller or larger than 0.5, meaning that one of the two directions was consistently more often chosen by perception or by pursuit. To investigate if the directional biases were consistent across observers and represent general biases or if they were idiosyncratic, the direction pairs were averaged across observers. The directional biases were mainly idiosyncratic, because for perception, average values across observers were only significantly different from 0.5 in the direction pairs left and down-left (back: 0.92 (±0.96), $t(9) = 2.45$, $P = 0.04$; front: 0.05 (±0.95), $t(9) = -3.02$,

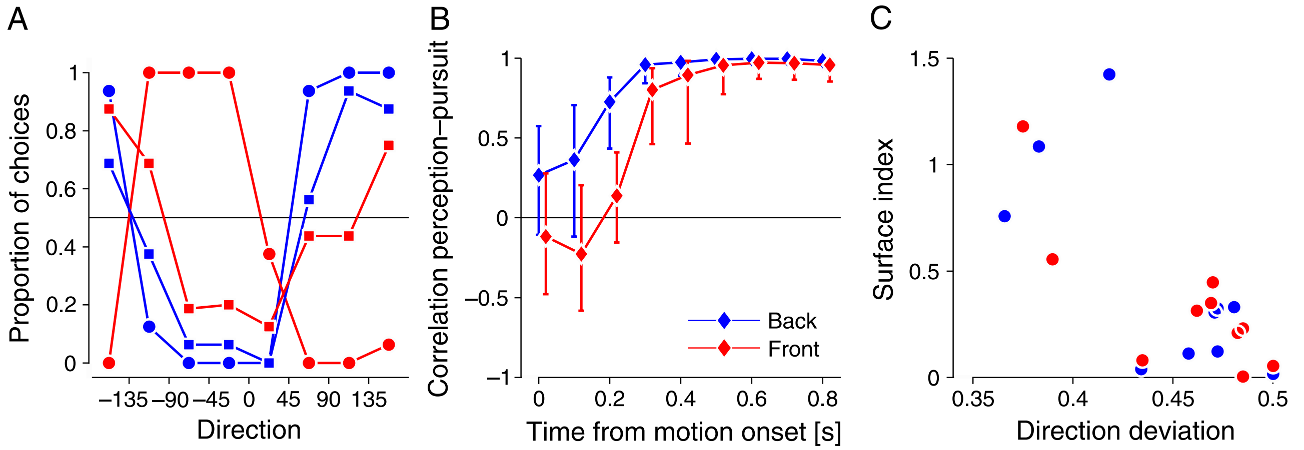

Figure 3. Experiment 1, influence of directional biases. (A) Proportion of choices for different pairs of motion directions when the surfaces had equal number of dots. Data of one exemplary observer are shown. (B) Average correlations across observers between direction biases of perception and pursuit separately for the front and back conditions. The values are horizontally offset to improve the visibility. (C) Perception: absolute value of surface index over direction deviation when the surfaces had equal number of dots. (A–C) Conventions are the same as in Figure 2.

P = 0.01) and down-right and right (back: 0.05 (±0.91), $t(9) = -4.19$, $P < 0.01$; front: 0.95 (±0.95), $t(9) = 3.10$, P = 0.01). In both cases, the horizontal motion was seen more often in the back than the diagonal motion. For pursuit 200 ms after motion onset, the direction pair left and down-left was significantly different from 0.5 but only in the front condition (0.12 (±0.92), $t(9) = -2.57$, P = 0.03). In this case, eye movements followed less often the diagonal motion. This shows that there were only few consistent directional biases across observers. For instance, there was no sign of a general oblique effect (Ball & Sekuler, 1987; Krukowski & Stone, 2005).

In order to investigate if direction biases were identical for perception and pursuit, we correlated both, separately for back and front conditions (Figure 3B). These correlations were significantly larger than zero for the back condition from 200 ms after motion onset and for the front condition from 250 ms onward. Strikingly, these correlations increased over time, with a time course very similar to the changes observed in the pursuit surface indices (Figure 2E). In addition, the increase of the correlations was delayed in the front condition relative to the back condition, like the changes in surface indices were delayed in the front condition. This indicates that directional biases for pursuit were initially independent from that for perception but became more similar afterward.

In order to investigate if the strength of directional biases constrained the effect of the dot number ratio, we calculated the root-mean-squared deviation from 0.5 with identical surfaces (Equation 5) and correlated it with the absolute value of the surface index. The direction deviation is zero, if all directions were equally often seen in the back and 0.5 if, in each direction pair, one direction is always seen in the back. For perception (Figure 3C), the direction deviations and absolute values of surface indices were highly negatively correlated (back: $r = -0.70$, P = 0.02; front: $r = -0.80$, P = 0.01), indicating that the direction bias constrained the effect of dot number. These data show that the influence of surface differences on perceived depth order was indeed limited by the strength of idiosyncratic direction biases. In other words, observers with weak directional biases showed strong effects of surface differences, while observers with strong directional biases showed only weak effects of surface differences. For pursuit, there was no significant correlation between surface indices and direction biases in any time window. Hence, directional biases did not constrain the influence of surface features for pursuit.

Experiment 2: Adaptation

Experiment 1 showed that the relative number of dots in the two surfaces influenced their perceived depth order. This is consistent with previous results showing that surfaces with higher spatial frequency are seen more often in the back (Moreno-Bote et al., 2008). However, the results of Experiment 1 can also be interpreted as evidence that the stronger motion tends to be seen in the back. That more dots lead to a stronger motion signal is supported by the fact that initial pursuit preferred the surface with more dots in Experiment 1. Another way to manipulate the strength of a motion signal is motion adaptation (Kohn & Movshon, 2003, 2004; Van Wezel & Britten, 2002). Previously, it has been shown that adaptation to transparent motion also influences unidirectional motion perception (Verstraten, Fredericksen, & van de Grind, 1994). It is also known that adaptation to an unambiguous rotation creates an aftereffect in an ambiguous rotation (Nawrot & Blake, 1991). Here, we wanted to investigate how unidirectional motion adaptation affects the perceived depth ordering of transparent motion.

To this end, observers adapted to a single surface moving leftward or rightward for 5 s, before they saw the transparent motion display (Figure 1B). The transparent motion had always one surface moving orthogonal to the adaptor and one surface moving either in the same direction as the adaptor (adapt) or in the opposite direction (opposite).

To account for the effects of adaptation, we extended the logit model by two parameters that shift the function horizontally, along the manipulated variable, here dot number (Equations 2 and 3). This model uses a common surface index for adapt and opposite conditions to estimate the general influence of dot number on perceived depth order. The adapt and opposite conditions are shifted horizontally by two separate parameters, the adaptation index opposite and adaptation index adapt, to estimate the influence of the adaptation procedure. A horizontal shift of the function assumes that adaptation affects perceived depth order and eye movement preferences only indirectly via the effect of dot number, whereas a vertical shift of the function would assume an independent effect of adaptation per se. The model used the same surface index for the adapt and the opposite condition, but different adaptation indices. With three free parameters (surface index, adaptation index opposite, and adaptation index adapt), the model explained on average 94.04% (±10.22) of the variability for perception and 95.36% (±5.92) for pursuit at 200 ms after motion onset. Since the model could explain the results of adaptation, using a horizontal shift, it is likely that adaptation acts only indirectly via the effect of dot number.

Like in Experiment 1, there was an effect of the distribution of dots to the two surfaces (Figure 4).

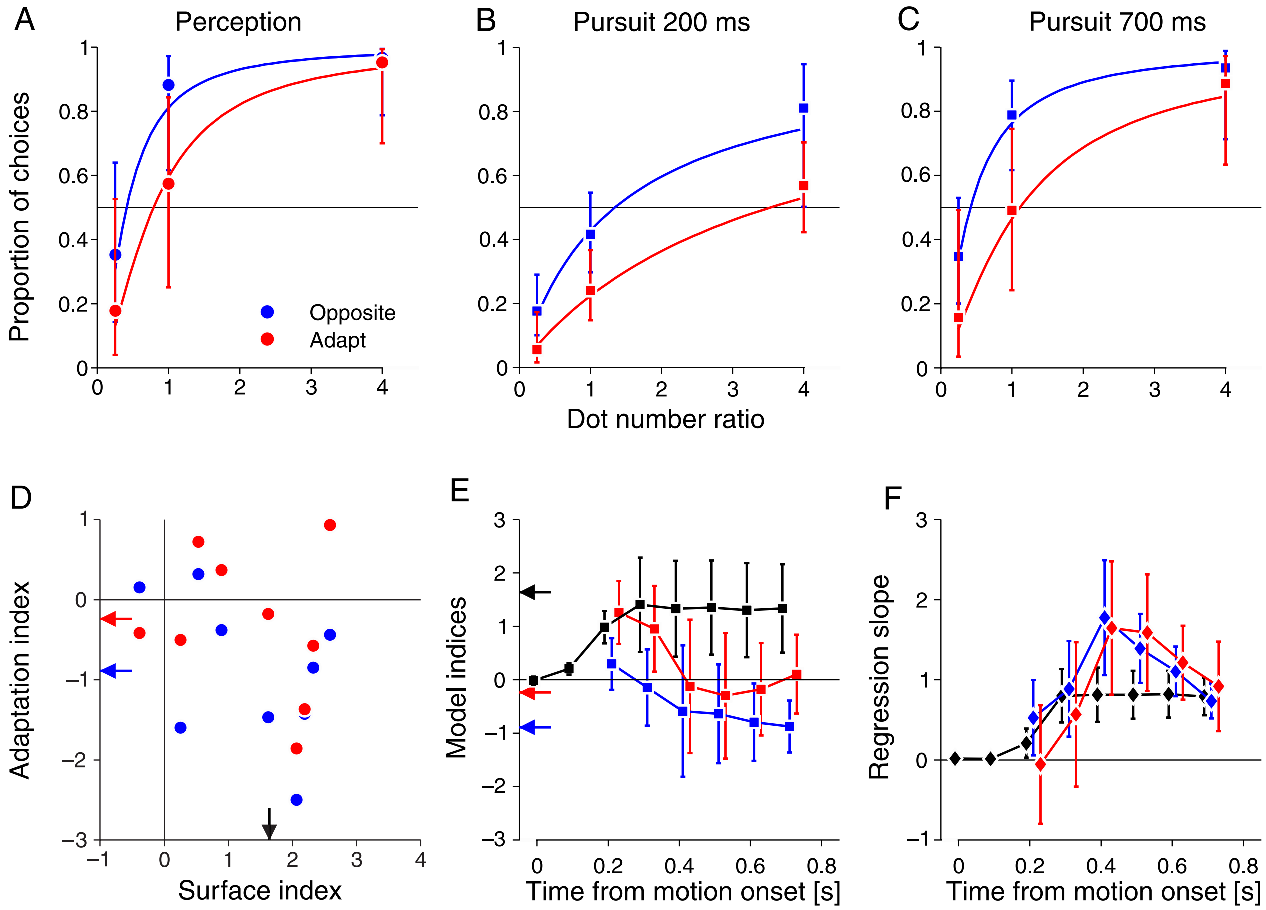

Figure 4. Experiment 2, influence of motion adaptation. (A–C) Average proportion of choices across observers. The lines are obtained by fitting the logit model from Equations 2 and 3. (A) Proportion of back judgments for adaptation and opposite conditions. (B, C) Proportion of pursuit choices 200 and 700 ms after motion onset. (D) Perceptual adaptation indices over surface index. (E) Average pursuit indices over time. (D, E) The arrows represent the average perceptual indices. (F) Slope of regression of pursuit indices on perceptual indices. (E, F) The adaptation indices are not shown before 200 ms, because they cannot be estimated reliably if the corresponding surface index is close to zero. The arrows represent the average perceptual indices. The values are horizontally offset to improve the visibility. (D–F) The surface index is plotted in black and the adaptation indices in the opposite and adapt conditions are plotted in blue and red, respectively. (A–F) Blue indicates conditions where directions opposite and orthogonal to the adaptor were tested; red indicates conditions where directions same as the adaptor and orthogonal to the adaptor were tested. Perception is indicated by circles; pursuit is indicated by squares. Error bars indicate 95% confidence intervals.

Perceptually, the surface containing more dots was seen more often in the back, as the average surface index for perception was 1.64 (±1.38) and significantly larger than zero ($t(9) = 3.77$, $P < 0.01$); 200 ms after motion onset, pursuit followed more often the surface containing more dots, since the surface index was 0.99 (±0.42) and also significantly larger than zero ($t(9) = 7.39$, $P < 0.01$). In contrast to Experiment 1, the surface index for pursuit reached a constant value 300 ms after motion onset and did not decline afterward (Figure 4E). Interestingly, it stabilized again on a value similar to perception. A regression of pursuit on perceptual surface indices revealed slopes significantly larger than zero from 200 ms onward (Figure 4F). This suggests that perceptual depth ordering had an earlier influence on pursuit choices than in Experiment 1. For perception, the surface index was significantly larger in Experiment 2 than in Experiment 1 ($t(9) = -3.01$, $P = 0.01$). For pursuit after 200 ms, it was not significantly different between the experiments ($t(9) = 0.41$, $P = 0.69$). The larger perceptual surface index in Experiment 2 might be caused by the larger angular separation of the surface (90° vs. 45°) or by the smaller number of possible motion directions (4 vs. 8).

In order to quantify the effects of the adaptation, we analyzed the adaptation index of the model. Perceptual choices were influenced by adaptation mainly in the opposite condition. Here, the adaptation index was −0.89 (±0.87) and significantly smaller than zero ($t(9) = -3.24$, $P = 0.01$). In the adapt condition, the adaptation index was −0.24 (±0.90) and did not differ significantly from zero ($t(9) = -0.82$, $P = 0.43$). This means that the surface moving opposite to the adaptor was seen more often in the back. Contrary to perceptual choices, initial pursuit choices were mainly influenced in the adapt condition. In this condition, the adaptation index was 1.26 (±0.82) and significantly larger than zero ($t(9) = 4.84$, $P < 0.01$). In the opposite condition, the adaptation index was 0.30 (±0.68) and did not differ from zero ($t(9) = 1.38$, $P = 0.20$). This means that the surface moving in the adapted direction was less often pursued. Unlike the constant surface index, the adaptation index changed over time for pursuit (Figure 4E). For both the adapt and the opposite conditions, the adaptation index declined over time, for the adapt condition to a value about zero, and for the opposite condition to a value significantly below zero. Both values were very similar to the corresponding adaptation indices for perception. Whereas in the beginning pursuit selected less often the adapted direction, at the end pursuit selected more often the opposite direction, both compared to an orthogonal direction. This means that in the beginning pursuit was mainly affected along the adaptation direction and later on it was mainly affected along the opposite direction. Hence, pursuit choices also became more similar to perception over time. This is also confirmed by the regression of pursuit on perception. Regression slopes were significantly larger than zero after 200 ms in the opposite condition and after 400 ms in the adapt condition (Figure 4F). Thus, it took the eyes longer to reflect the perceptual preferences in the adapt condition.

The results of this experiment show that motion adaptation affects perceived depth ordering and eye movement choices in transparent motion. Motion opposite to adaptation was seen more often in the back and the adapted motion direction was less often selected by initial pursuit. These effects of adaptation could be modeled by a horizontal shift of the function, along the dot number ratio axis. This suggests that either adaptation influences perceived depth order by manipulating the effect of dot number or that there is a third factor responsible for both effects of dot number and adaptation.

Experiment 3: Speed

Experiment 2 replicated the influence of dot number on perceived depth order from Experiment 1 and additionally showed that the adapted motion direction was seen less often in the back than the opposite motion direction. This could be interpreted as evidence that a weaker motion signal is seen less often in the back, since motion adaptation reduces neural activity in area MT (Kohn & Movshon, 2003, 2004; Van Wezel & Britten, 2002). However, motion adaptation also has a couple of other effects. On a neuronal level, it changes not only the responsiveness of MT neurons but also their directional tuning (Kohn & Movshon, 2003, 2004). On a behavioral level, adaptation can increase or decrease the perceived speed, depending on the relative speed of adaptor and test (Smith & Edgar, 1994). Since in Experiment 2, the adaptor had the same speed as the surfaces, one can assume that the perceived speed of the surface moving in the same direction was reduced (Smith, 1985; Thompson, 1981). The available data for the influence of speed on the perceived depth order of transparent motion are inconsistent. One study found no influence of speed on the depth ordering (Mamassian & Wallace, 2010), while another study found that the fast surface is seen in the back (Moreno-Bote et al., 2008). Hence, we tested how depth order and pursuit choices are influenced by the speed difference of the two surfaces. The average speed of the two surfaces was kept constant at 10 deg/s and their speed ratio was varied from 1 to 4.

Our data showed a clear dissociation between perception and initial pursuit (Figure 5). While there was a strong tendency to see the faster moving surface less often in the back, initial pursuit tended to follow the faster surface. For perception, the average surface index was −1.73 (±1.29) and significantly smaller than zero ($t(9) = -4.24$, $P < 0.01$). For pursuit, the average surface index was 0.70 (±0.34) and significantly larger than zero ($t(9) = 6.53$, $P < 0.01$). Like in Experiments 1 and 2, pursuit behavior became more similar to perception over time: The pursuit surface index reached a positive peak at 200 ms and then gradually declined to a value below zero

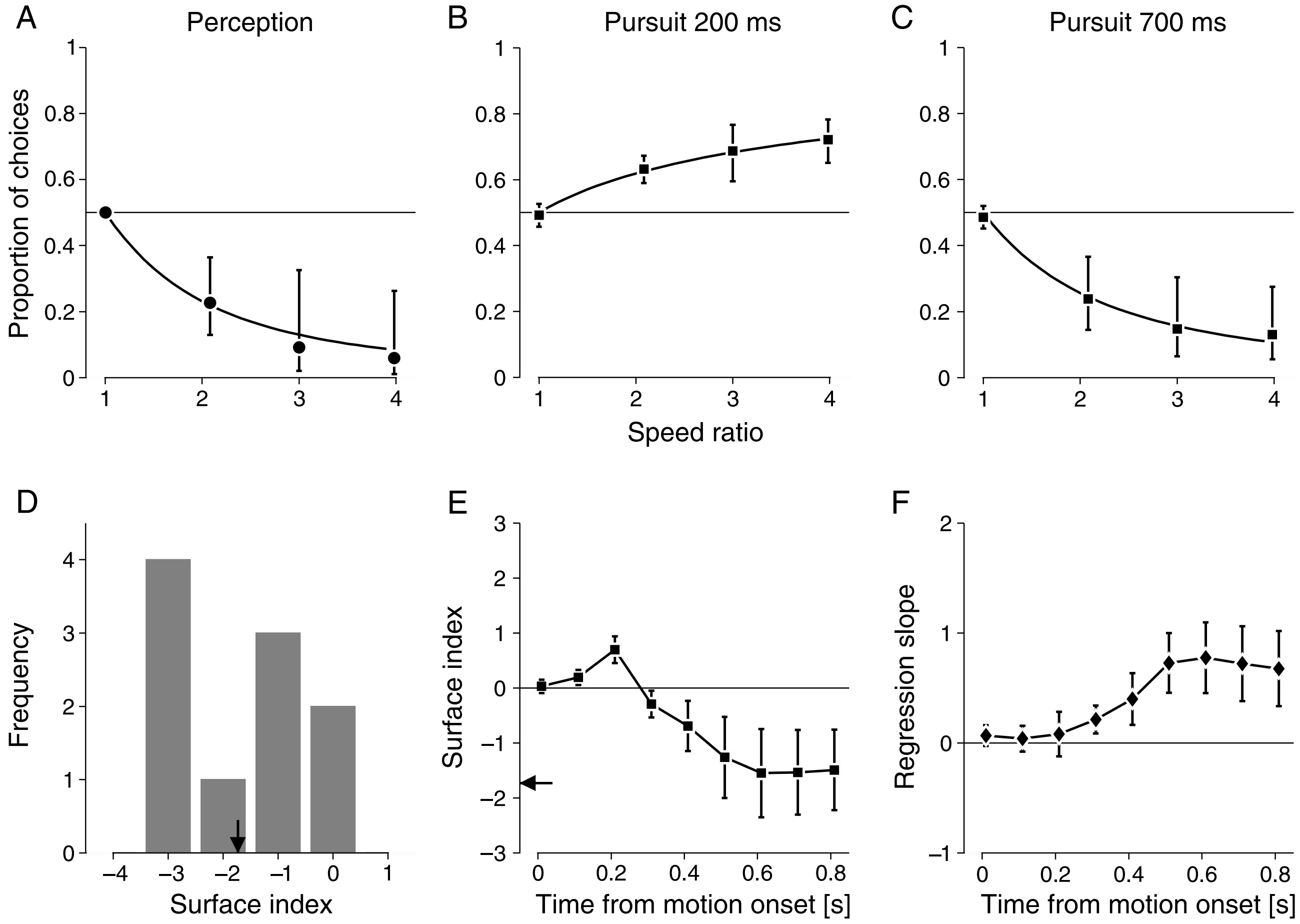

Figure 5. Experiment 3, influence of motion speed. (A–C) Average proportion of choices across observers. The lines are obtained by fitting the logit model from Equation 1. (A) Proportion of back judgments. (B, C) Proportion of pursuit choices 200 and 700 ms after motion onset. (D) Histogram of perceptual surface indices. (E) Average pursuit surface index over time. (D, E) The black arrow represents the average perceptual surface index. (F) Slope of regression of pursuit surface index on perceptual surface index. (A–F) Perception is indicated by circles; pursuit is indicated by squares. Error bars indicate 95% confidence intervals.

(Figure 5E) and a regression of pursuit surface index on perceptual surface index showed a slope larger than zero after 300 ms (Figure 5F).

Like in Experiment 1, we calculated the magnitude of directional biases of perceived depth order (Equation 5) in trials with no speed difference and correlated it with the perceptual surface index. In contrast to Experiment 1, there was no significant correlation ($r = -0.46$, $P = 0.18$). This means that the influence of the speed differences on perceived depth order was not constrained by the directional biases.

Since observers saw the slower moving surface in the back, it is unlikely that the effect of dot number in Experiments 1 and 2 is mediated by speed. Adding more dots to a surface should increase its perceived speed, as shown by studies on pursuit (Heinen & Watamaniuk, 1998; Schütz et al., 2010) and motion perception (Schütz et al., 2010). The adaptation effect in Experiment 2 is also not consistent with the observed speed dependency. If anything, adaptation should reduce the perceived speed of the surface moving in the adapted direction, but this surface was seen less often in the back. Hence, speed differences between the surfaces cannot account for the effect of dot number or adaptation on the perceived depth order.

Experiment 4: Dot density

In Experiments 1 and 2, the variation of dot number was confounded with a variation of dot density, since the aperture size was constant. Thus, it is possible that the effects of dot number were actually caused by dot density. To measure the influence of dot density alone, we kept the dot number in the two surfaces constant and varied their aperture size to yield dot density ratios of 1 to 4.

The data showed little influence of dot density (Figure 6): There was only a non-significant trend to perceive the more dense surface in the back and initial pursuit was completely unaffected by dot density. For perception, the

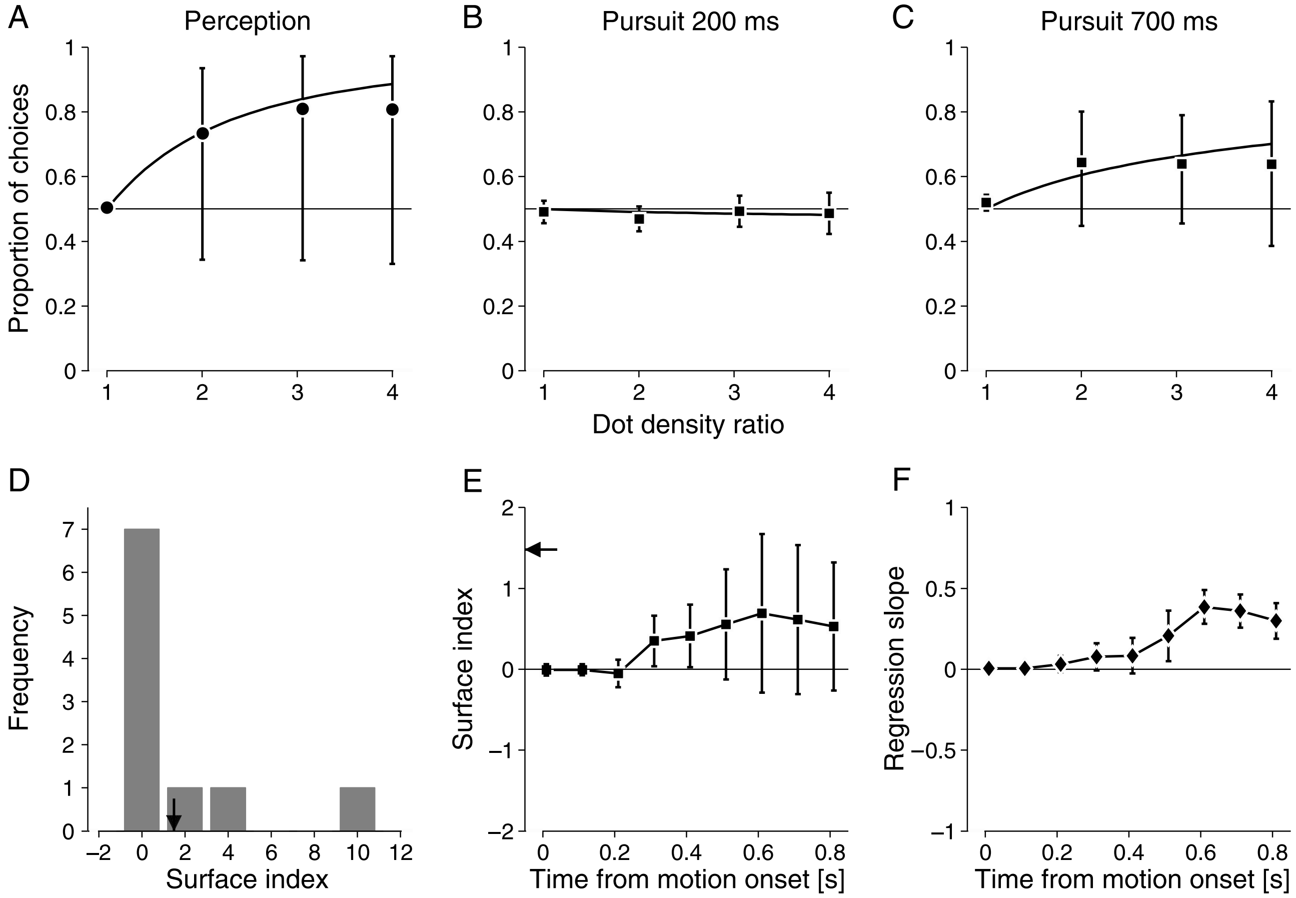

Figure 6. Experiment 4, influence of dot density. (A–C) Average proportion of choices across observers. The lines are obtained by fitting the logit model from Equation 1. (A) Proportion of back judgments. (B, C) Proportion of pursuit choices 200 and 700 ms after motion onset. (D) Histogram of perceptual surface indices. (E) Average pursuit surface index over time. (D, E) The black arrow represents the average perceptual surface index. (F) Slope of regression of pursuit surface index on perceptual surface index. (A–F) Conventions are the same as in Figure 5.

average surface index was 1.48 (±3.38) and not significantly different from zero ($t(9) = 1.39$, $P = 0.20$). Moreover, the average surface index was biased by one observer, who had an extreme surface index of 10.25 (Figure 6D). Without this observer, the average surface index was 0.51. Hence, the dot density did not influence the perceived depth order. There was no correlation between the surface indices for dot number in Experiment 1 and the surface indices for dot density in this experiment ($r = -0.17$, $P = 0.65$). This also suggests that the effect of dot number was not caused by dot density.

The average surface index for pursuit was −0.05 (±0.24) and not significantly different from zero ($t(9) = -0.70$, $P = 0.50$). The surface index for pursuit increased over time but was only significantly larger than zero from 300 to 400 ms after motion onset (Figure 6E). The regression of pursuit on perceptual surface index revealed a very late influence of perception after 500 ms (Figure 6F), which is 200 ms later than in Experiments 1 and 3.

Since there was no correlation between the perceptual surface index and the magnitude of directional biases ($r = 0.27$, $P = 0.45$), the perceptual effects of dot density were not constrained by the directional biases.

Experiment 5: Dot size

Experiment 1 showed that the surface containing more dots is seen more often in the back. This could imply that the stronger motion is seen in the back or, alternatively, that the surface is seen in the back, in which the illuminated area, i.e., the area filled by the dots, is larger. A way to test this pictorial influence is to use different dot sizes. Following the laws of perspective, also the size of the individual dots should influence the perceived depth ordering. Smaller dots should be seen in the back and larger dots should be seen in the front (Moreno-Bote et al., 2008). To test this, we varied the ratio of the dot area from 0.1 to 1.8.

Unexpectedly, our data showed a clear effect of dot size only for pursuit but not for perception (Figure 7). Initial pursuit followed preferentially the surface with larger

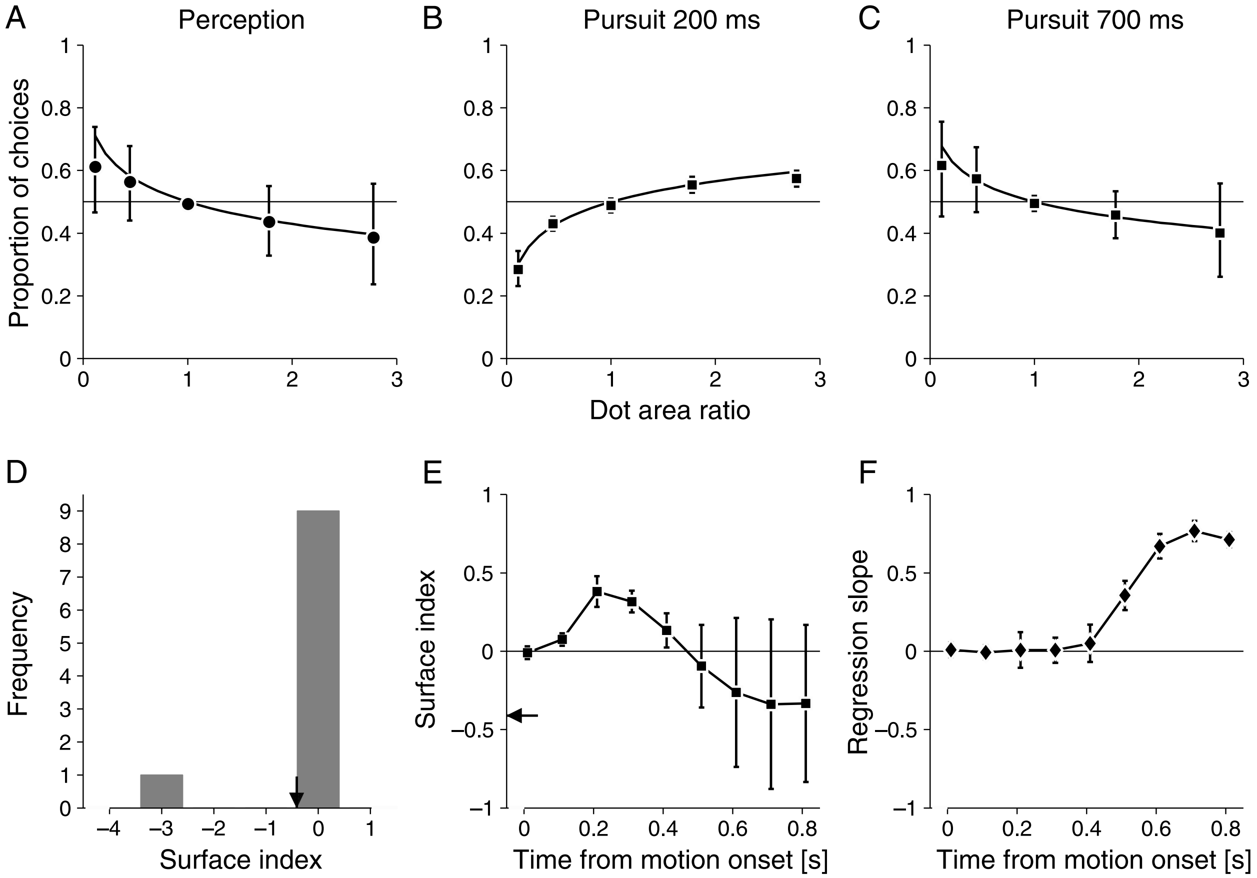

Figure 7. Experiment 5, influence of dot size. (A–C) Average proportion of choices across observers. The lines are obtained by fitting the logit model from Equation 1. (A) Proportion of back judgments. (B, C) Proportion of pursuit choices 200 and 700 ms after motion onset. (D) Histogram of perceptual surface indices. (E) Average pursuit surface index over time. (D, E) The black arrow represents the average perceptual surface index. (F) Slope of regression of pursuit surface index on perceptual surface index. (A–F) Conventions are the same as in Figure 5.

dots, which only tended to be seen less often in the back perceptually. For perception, the average surface index was −0.41 (±0.98) and not significantly different from zero ($t(9) = -1.32$, $P = 0.22$). Moreover, the average surface index was extremely affected by one observer, who had a surface index of −3.16 (Figure 7D). Without this observer, the average surface index was −0.10. Hence, the dot size did not influence the perceived depth order. The average surface index for pursuit was 0.38 (±0.14) and significantly larger than zero ($t(9) = 8.81$, $P < 0.01$). Like in the previous Experiments 1 and 3, the surface index had a peak after 200 ms and then became more similar to the perceptual bias over time (Figure 7E). The regression of pursuit on perceptual surface index revealed a very late influence of perception after 500 ms (Figure 7F), like in Experiment 4. This is not surprising since the effects of dot size on perception were very small and presumably have only small influence on pursuit.

In this experiment, the perceptual surface index was highly correlated with the magnitude of directional biases ($r = -0.95$, $P < 0.01$). Hence, the perceptual effects of dot size were constrained in the same way by directional biases as the effects of dot number in Experiment 1.

Experiment 6: Eye movements

Across all previous experiments, there was no match between perceived depth order and the surface preferences by initial smooth pursuit eye movements. This indicates that the choice of eye movements did not determine perceived depth order alone. However, over time eye movement choices became similar to the attended surface. This change in eye movement direction might be a top-down influence of attention, as previously suggested (Mestre & Masson, 1997; Watanabe, 1999). However, it is not clear if the change in eye movement direction is necessary and how it affects perceived depth order. Thus, in a final experiment, we experimentally manipulated the direction of smooth pursuit to test if the change in eye movement direction is necessary for the depth ordering. Observers had to follow a red bull's-eye, which was

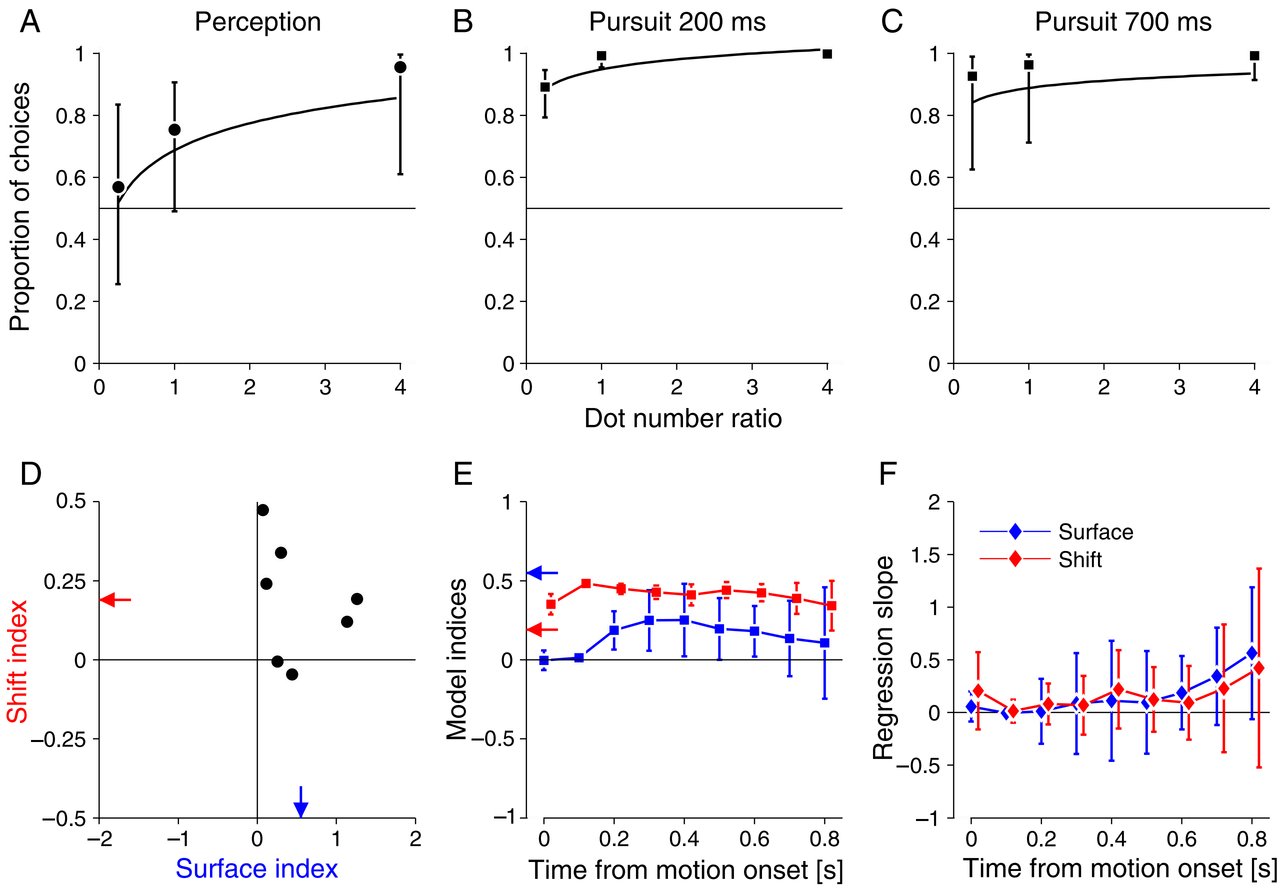

Figure 8. Experiment 6, influence of eye movements. (A–C) Average proportion of choices across observers. The lines are obtained by fitting the extended logit model from Equation 4. (A) Proportion of back judgments. (B, C) Proportion of pursuit choices 200 and 700 ms after motion onset. (D) Perceptual shift index over surface index. (E) Average pursuit indices over time. (D, E) The blue and red arrows represent the average perceptual surface and shift indices, respectively. (F) Slope of regression of pursuit indices on perceptual indices. (E, F) The values for surface and shift indices are horizontally offset to improve the visibility. Time is given relative to the onset of the transparent motion. Motion onset of the eye movement target was 200 ms earlier. (A–F) Perception is indicated by circles; pursuit is indicated by squares. Error bars indicate 95% confidence intervals.

moving in the same direction as one of the surfaces. To facilitate smooth pursuit initiation, the eye movement target made a 2-deg step opposite to its motion direction (Rashbass, 1961) and moved for 200 ms before the transparent motion appeared. The relative number of dots was varied in ratios of 0.2, 1, and 4. To quantify the effect of the eye movements, we used an additional shift index (Equation 4), which shifts the function along the vertical axis.

Both perceived depth order and pursuit were influenced by the instruction to follow the pursuit target. The surface moving in the same direction as the eye movement target was seen more often in the back and was almost always followed by pursuit (Figure 8). However, perceived depth order was also still influenced by the number of dots in the surfaces.

For perception, the surface index was, on average, 0.51 (±0.49) and significantly larger than zero ($t(6) = 2.77$, $P = 0.03$). For pursuit 200 ms after transparent motion onset, the surface index was 0.19 (±0.13) and significantly larger than zero ($t(6) = 3.78$, $P = 0.01$). Surface indices for pursuit were significantly larger than zero in the time intervals 200, 300, 400, and 600 ms after transparent motion onset (Figure 8E) but remained on the same low level (0.18–0.25). This indicates that the surface differences in terms of dot number had an influence on perceived depth order, even if pursuit eye movements were linked to one of the surfaces and showed only little influence of dot number. There were no significant regressions of pursuit surface index on perceptual surface index (Figure 8F), which also supports the notion that the effect of dot number was independent of the eye movements.

To investigate the direct influence of the eye movements, we analyzed the shift index. The shift index for perception was 0.19 (±0.18) and significantly larger than zero ($t(6) = 2.69$, $P = 0.04$). The shift index for pursuit was 0.45 (±0.03) and significantly larger than zero ($t(6) = 34.43$, $P < 0.01$). It stayed on a constant value of about 0.45 for the whole trial (Figure 8E). There was no significant regression of pursuit shift index on perceptual shift index (Figure 8F). Interestingly, neither the surface nor the shift indices for pursuit adjusted to the values of perception. These results suggests that eye movements can bias the initial depth ordering in transparent motion, independently of the effects of surface differences.

Discussion

In six experiments, we investigated how different manipulations influence perceived depth order and smooth eye movements in transparent motion. The results for perception showed that some surface differences can bias the ambiguous depth ordering in transparent motion (Figure 9A): Surfaces containing more dots (Experiments 1, 2, and 6), moving opposite to an adapted direction (Experiment 2), or moving at a slower speed (Experiment 3) were seen more often in the back. There was no significant influence of dot density (Experiment 4) or dot size (Experiment 5) on perceived depth order, but there was a bias to see surfaces in the back that moved in the same direction as the eyes (Experiment 6).

In most experiments, initial pursuit showed clear preferences for one of the two surfaces (Figure 9B and 9C): Initial pursuit preferred the surface containing more dots (Experiments 1 and 2), moving in a non-adapted direction (Experiment 2), moving at a faster speed (Experiment 3), or being composed of larger dots (Experiment 5). Only the dot density had no influence on initial pursuit (Experiment 4). Later pursuit followed in general either the surface perceived in the back or perceived in the front, depending on the perceptual task (Experiment 1).

Perceived depth order and eye movements

Considering the important role of smooth pursuit for motion parallax (Nadler et al., 2008, 2009; Naji & Freeman, 2004; Nawrot & Joyce, 2006), it is an interesting question if eye movements also affect depth ordering in motion transparency.

Three arguments speak against a direct causal influence of eye movements on perceived depth order. First, across experiments, perceived depth order and initial eye movement preferences did not follow a consistent pattern. When the relative number of dots in the surfaces was varied (Experiments 1 and 2), initial eye movement preferences were aligned with the surface perceived in the back. When the speed of the surface was varied (Experiment 3), they were aligned with the surface perceived in the front, and when the size of the dots was varied (Experiment 5), eye movements showed a significant preference for the surface with larger dots, whereas perceived depth ordering remained ambiguous. These discrepancies between perception and pursuit across experiments indicate that initial eye movements did not moderate the influence of surface features on perceived depth order. The second argument against a causal influence of eye movements comes from eye movement behavior over time. Within each experiment, the regressions of pursuit on perception showed typically late effects, after the surface indices peaked for pursuit. This shows that eye movements were independent of perception in the beginning of a trial and showed agreement with perception only later in a trial. The third argument against a causal role of eye movements is based on the observation of directional biases. In Experiment 1, there were strong idiosyncratic directional biases of perceived depth order, like described previously (Mamassian &

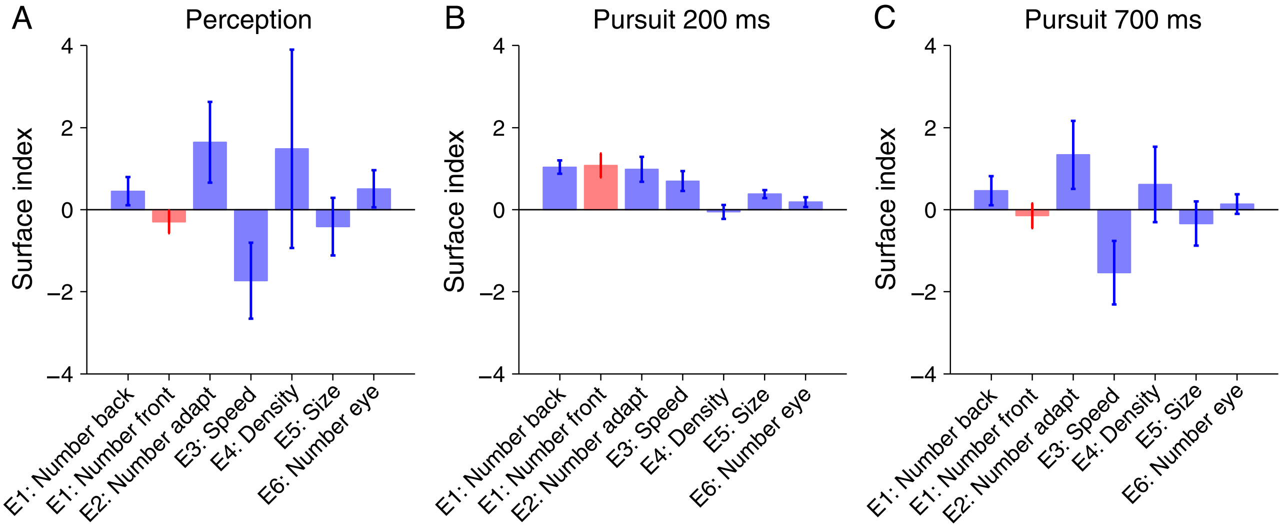

Figure 9. General results across experiments. (A–C) Average surface indices across observers. Conditions with back and front judgments are plotted in blue and red, respectively. (A) Perception. (B) Pursuit 200 ms after transparent motion onset. (C) Pursuit 700 ms after transparent motion onset.

Wallace, 2010). Interestingly, the directional biases of perceptual depth ordering were different from the directional biases for initial pursuit. These three observations suggest that the depth order in motion transparency might be either determined by a different neural network than smooth pursuit eye movements, or by the same neural network, but at a different time, when the network is in a different state.

On the other hand, Experiment 6 showed that eye movements can influence perceived depth order: The surface moving in the same direction as the eye movements was seen more often in the back. Since this effect was independent of the effect of dot number in the two surfaces, eye movements exhibit either a direct influence on perceived depth ordering or their influence is mediated by a factor other than dot number.

A possible mediating factor might be speed, as suggested previously (Maruyama et al., 2003). Experiment 3 showed that speed has a strong influence on perceived depth order, so that the slower surface is perceived in the back. A remaining question is at which stage of motion processing the interaction with depth order occurs. It might be that the interaction occurs early in the motion processing, where eye movements are not yet compensated for. As a result, only the retinal speed of the surfaces would matter. If this is the case, the surface that attracts initial eye movements should be consistently perceived in the back, since its retinal speed will be strongly reduced. The results of Experiment 5 are not completely consistent with that idea, because the surface with larger dots was preferred by initial eye movements but not consistently seen in the back. Likewise, in Experiment 3, eye movements followed initially the faster surface, thereby effectively reducing its retinal speed. Nevertheless, the faster surface was seen in front of the other. Another possibility would be that the interaction between speed and depth order occurs later, after the eye movements are incorporated into the estimation of speed. Moving targets are typically perceived to move slower when they are pursued (Aubert, 1886; Fleischl, 1882; Freeman, Champion, & Warren, 2010). As a result, the surface followed by the eyes will have a slower perceived speed than the other surface and thus will be perceived in the back.

Directional biases of depth ordering and eye movements

Previous results showed that there are sustained biases to see down- and rightward motion in front (Mamassian & Wallace, 2010). Since we did not measure 180° direction separations of motion components, it is difficult to compare our results. We also found consistent directional biases across observers to see horizontal motion more often in the back, compared to diagonal downward motion. However, most of the directional biases in our study differed between observers and thus were idiosyncratic. As mentioned above, these directional biases were not correlated between perception and initial pursuit.

The magnitude of these directional biases was negatively correlated with the surface effects of dot number and dot size. There was no correlation with the effects of speed or dot density. These results indicate that some of the tested surface features (dot number and dot size) were constrained by directional biases, whereas other features (speed or dot density) were independent of directional biases. This difference between surface features might indicate that there is a hierarchy of weaker and stronger cues for perceived depth in transparent motion and that some cues can override others. Since directional biases can be overridden by some cues, one could argue that motion direction acts as a cue for depth order just like the other surface differences. Further studies might investigate how inconsistent cues are weighted against each other and if the associations between surface features and depth order can be manipulated, as it has been shown for directional biases (Chopin & Mamassian, 2011).

Perceptual effects of dot number and adaptation

Experiments 1 and 2 showed that the surface containing more dots is seen more often in the back. In Experiment 2, the effect of dot number was additionally modulated by the adaptation state of the two motion directions: The surface moving opposite to the adaptor was seen more often in the back. These two effects are probably not independent of each other, because the effects of adaptation could be modeled by a horizontal shift of the function and not by a vertical shift. In the following, we want to discuss potential common causes for the effects of dot number and adaptation on perceived depth order. Adding more dots to a surface, of course, changes several properties of that surface at the same time, and motion adaptation also might have several effects. First, the area covered by a surface increases with dot number. Since Experiment 5 showed no influence of dot size on depth order, we can exclude this factor. Second, the perceived speed of a surface might increase with dot number and decrease as a result of adaptation. An increase of speed with dot number would be consistent with the decrease of pursuit latency and increase of pursuit acceleration with dot number (Heinen & Watamaniuk, 1998). A reduction of speed by adaptation would be also consistent with the literature (Smith, 1985; Smith & Edgar, 1994; Thompson, 1981). However, Experiment 3 showed that the faster surface is seen in the front and not in the back. This means that the effects of dot number and adaptation on depth order were in the wrong direction. Third, the spatial frequency of a surface increases with dot number, which has been shown to increase the tendency to see the surface in the back (Moreno-Bote et al., 2008). However, it is unclear how motion adaptation should lead to a direction-specific change in apparent spatial frequency. Moreover, Experiment 4 showed no consistent influence of dot density on perceived depth order. Fourth, both effects of dot number and adaptation could be mediated by eye movements, as described in the previous section. However, in Experiment 6, eye movements created a bias, which was independent of the effect of dot number (Equation 4), whereas the effect of adaptation was not independent of dot number (Equations 2 and 3). Furthermore, in Experiment 2, the surface moving opposite to the adaptor was seen more often in the back, whereas initial pursuit followed the adapted direction less often. Surfaces moving in the same or in the opposite direction of the adaptor were presented in different trials. Hence, it is unlikely that the effects of adaptation on perceived depth order were mediated by eye movements. Finally, it might be that dot number and adaptation modulate neural activity of motion-sensitive neurons. The surface that has more dots or that is moving opposite to an adapted direction presumably generates more neural activity. In this view, the current results would indicate that the stronger surface is seen in the back. It would be interesting to see if not only perceived depth but also the apparent dot number is affected by adaptation.

Perceptual effects of speed

The available data on the influence of speed on depth ordering are inconsistent. Our data show that the faster surface was consistently seen more often in the front. A previous study found that the faster moving surface was seen more often in the back (Moreno-Bote et al., 2008). At least four methodological differences could be responsible for the different results. First, the previous study measured dominance times during 60-s presentations, while the current study only measured the initial depth ordering. It might be that the initial depth ordering follows a different bias than the dominance times during prolonged exposure. For binocular rivalry, it has already been shown that the initial percept can differ from later switches (Carter & Cavanagh, 2007). Second, the two studies differ in how much they emphasize the use of single features. The dots in the previous study were relatively large (0.36 deg) and had an unlimited lifetime, while the dots in the current study were small (0.14 deg) and had a lifetime of 200 ms. Thus, the current stimulus required global motion processing, while the stimulus in the previous study allowed observers to focus on individual features. The assumption that our stimulus minimized the influence of single features is also supported by the fact that dot size did not influence depth ordering in our results, while it was effective in the previous study (Moreno-Bote et al., 2008). Third, the observers were free to move their eyes in the current study, while the previous study used a fixation spot (Moreno-Bote et al., 2008). It is possible that the execution of eye movements and the accompanying changes of retinal and/or perceived speed affected depth judgments. Fourth, the presence of a fixation spot might have determined the fixation plane. The fixation spot was drawn on top of the transparent motion stimuli, so that the transparent motion was displayed behind the current fixation plane. Faster motion indicates that a surface is further away from fixation, i.e., in this case behind the slower moving surface. In the current experiment, the fixation plane was not defined by a fixation point. Since observers saw the faster motion in front, it is most likely that here the fixation plane was behind the transparent surfaces.

Another study investigating motion transparency depth rivalry found no effect of speed on the depth ordering (Mamassian & Wallace, 2010). Two methodological differences might account for the difference in results. First, Mamassian and Wallace used very short presentation durations of 280 ms. It might be that such a short motion duration is not sufficient to drive eye movements. In this case, the change of retinal and/or perceived speed, induced by the eye movements in our study, might be responsible for the different perceptual results. Moreover, the surface preferences of eye movements in Experiment 3 changed from the faster surface to the slower surface after about 300 ms, i.e., later than the motion duration in Mamassian and Wallace's study. This change in eye movement preferences might be caused by a top-down, task-dependent signal, reflecting the perceived depth order. If this is true, speed differences presumable need more than 300 ms to effectively determine perceived depth order. Second, in the previous study, the two surfaces were additionally distinguished by black and white dots and observers had to indicate the luminance polarity of the surface moving in front. It might be that this surface difference and the associated response type also increased the focus on single dots, with the result that the speed of the whole surface was neglected.

Surface effects on eye movements

The finding from Experiment 1 that initial pursuit preferred the surface containing more dots is consistent with data showing that initial pursuit follows the vector average (Lisberger & Ferrera, 1997) and with data showing that initial acceleration of pursuit increases with dot number or density (Heinen & Watamaniuk, 1998) and motion coherence (Schütz et al., 2010). The finding from Experiment 2 that initial pursuit followed the surface moving in an adapted direction less often is consistent with previous reports showing repulsion of post-saccadic pursuit direction and speed from the adapted direction and speed (Gardner, Tokiyama, & Lisberger, 2004) as well as the reduction of initial pursuit acceleration (Taki, Miura, Tabata, Hisa, & Kawano, 2006). Furthermore, pursuit can also be elicited by motion aftereffects (Braun, Pracejus, & Gegenfurtner, 2006; Watamaniuk & Heinen, 2007).

Whereas initial pursuit choices were independent of the perceptual depth ordering, they became more similar to the perceptual judgments over time. In order to report the motion direction of the surface in front or in the back, observers presumably have to attend the surface in question. Previous data on optokinetic nystagmus (Mestre & Masson, 1997; Watanabe, 1999) suggest that attention as a top-down signal can determine which surface guides the eye movements. Experiment 1 showed that attention can be directed to the surface, which is perceived in the back or in the front and that pursuit follows the selected depth plane, similar to optokinetic nystagmus (Maruyama et al., 2003). These results suggest that the eyes initially stabilize the dominant motion signal and only later on follow the attended motion signal. In this view, one could argue that while the initial eye movements represent a more reflexive response, the later eye movements rather represent a volitional selection of the attended surface.

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