

Motion correspondence in the Ternus display shows feature bias in spatiotopic coordinates

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How is the visual system able to maintain object identity as the objects or the eyes move? While many early studies have shown small or no influence of feature information on this correspondence process, more recent studies have shown large feature effects. Here we investigated if this incongruity might be due to the distance over which the feature influence has an effect. We used a variation of the Ternus display (Ternus, 1926), an ambiguous apparent motion display, in which two sets of three discs are presented and one can perceive either three discs moving together (*group motion*) or one disc jumping across the other two discs (*element motion*). We biased the percept toward element motion by matching the features of some of the discs. In **Experiment 1**, with the three discs aligned and moving vertically, we added a horizontal offset between the two sets of discs and found a strong bias toward element motion that decreased with increasing spatial offset. In **Experiment 3** participants had to make horizontal saccades across the same Ternus displays so that the two Ternus frames were horizontally offset on the retina, but not in spatiotopic coordinates. We found that the bias showed a similar spatial range, but now it was clear that the range was set in spatial coordinates independently of the retinal position. These results show that feature information contributes to correspondence over a limited spatial range (**Experiment 1**) and that the range is imposed in spatial, not retinal, coordinates (**Experiment 2**).

Key Words: motion correspondence, apparent motion, Ternus display, spatiotopic processing, retinotopic processing

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Introduction

The sensory input that our visual system receives is neither continuous nor unambiguous. For example, if we try to keep track of the balls a juggler is tossing in the air (**Figure 1**), our visual system needs to track the path of each ball, determining which current positions correspond to which previous ones. This is not an easy task because objects occasionally disappear behind other objects and because we constantly move our eyes, and so change the location of all the objects on the retina. The question of how the visual system can establish and maintain the identity of an object under these circumstances has been named the *correspondence problem* (Ullman, 1979).

How the visual system solves this correspondence problem has been the focus of research for decades (Berbaum, Lenel, & Rosenbaum, 1981; Burt & Sperling, 1981; Casco, 1990; Dawson, Nevin-Meadows, &

Wright, 1994; Green, 1986; Kolers & von Grünau, 1976; Kolers & Pomerantz, 1971; Kramer & Rudd, 1999; Navon, 1976; Petersik & Rice, 2008). Researchers have used different types of apparent motion displays, from simple apparent motion displays, in which only two objects are presented (Berbaum, et al., 1981; Kolers & von Grünau, 1976; Kolers & Pomerantz, 1971), up to more complicated displays, in which multiple elements are presented in different frames and apparent motion can be seen between different elements (Burt & Sperling, 1981; Green, 1986; Navon, 1976; Nishida & Takeuchi, 1990; Nishida, Ohtani, & Ejima, 1992; Pooresmaeili, Cicchini, Morrone, & Burr, 2012; Shechter, Hochstein, & Hillman, 1988; Ullman, 1979). An example of a more complicated apparent motion display is the motion quartet (Navon, 1976; Schiller, 1932; Ullman, 1979), in which two discs are presented in diagonally opposite corners of a virtual rectangle (or diamond) in the first frame and another set of two discs in the other two corners in the second frame. In this

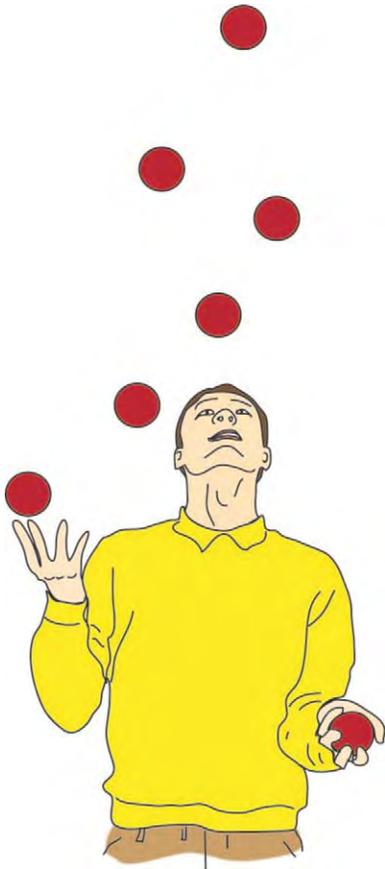


Figure 1. The correspondence problem in juggling (accurate drawing based on a photo). Our visual system needs to be able to know which ball went where in order for us to appreciate the juggler's performance.

display observers can either perceive two discs that are moving horizontally or two discs that are moving vertically. The direction of the perceived movement indicates which stimuli have been matched together.

In order to examine the correspondence process in these apparent motion displays, different factors have been manipulated, for example the spacing and timing between elements, as well as the features of the different objects (Navon, 1976; Ullman, 1979; Ramachandran & Anstis, 1983). In the motion quartet, the distance and the interstimulus interval (ISI) between the discs in the sequential frames strongly biases what motion direction is seen, whereas featural aspects, such as luminance, color, texture, or size seem to play a much smaller role (Navon, 1976; Schiller, 1932). This general pattern is seen for a range of different apparent motion displays, even though the conclusions concerning the importance of features compared to spatiotemporal factors are more varied. Some studies show no or small effects of features and underline how easily correspondence can be established between elements that are dissimilar (Burt & Sperling, 1981; Cavanagh, Arguin, & von Grünau, 1989; Navon, 1976; Nishida & Takeuchi,

1990; Nishida et al., 1992; Kolers & von Grünau, 1976; Kolers & Pomerantz, 1971; Werkhoven, Sperling, & Chubb, 1993, 1994), while other studies show at least some effect of features and underline the importance of feature information to determine correspondence (Berbaum et al., 1981; Green, 1986, 1989; Sekuler & Bennett, 1996; Shechter et al., 1988; Watson, 1986).

More recently studies have shown very robust biases from features for the motion seen in the Ternus display (Ternus, 1926; Pikler, 1917), where featural aspects can influence correspondence dramatically (Casco, 1990; Dawson et al., 1994; Hein & Moore, 2012; Kramer & Rudd, 1999; Kramer & Yantis, 1997; Petersik & Rice, 2008; Wallace & Scott-Samuel, 2007). In the typical Ternus display, three horizontally aligned discs are presented in alternation with a second set of three discs that are shifted horizontally by one position. Depending on how correspondence has been established between these different discs (Figure 2), all discs are perceived as moving together as a group (*group motion*) or one disc (disc A in Figure 2) appears to jump across the two other discs that are perceived as stationary (*element motion*).

If all the discs are the same, correspondence is strongly influenced by the contrast between Ternus discs and background, disc duration, and the ISI (Pantle & Picciano, 1976; Petersik & Pantle, 1979). For example, the longer the ISI, the more likely one is to perceive group motion. In accordance with these findings, it has been proposed that the two different motion percepts in the Ternus display, i.e., group and element motion, could be related to two different motion processes: a short-range (or low-level, as the stimuli engage low-level direction selective motion units) motion process responsible for element motion versus a long-range (or high-level, as the stimuli are too distant to engage low-level motion units) motion process, responsible for group motion (Pantle & Picciano, 1976; Petersik & Pantle, 1979). Even though this two-process explanation of the Ternus motion has been challenged (Breitmeyer & Ritter, 1986a; Odic & Pratt, 2008; but see Petersik, 2010), most other theories of the Ternus display have focused on a low-level

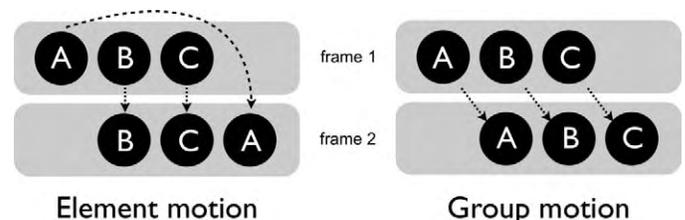


Figure 2. Two possible solutions to the correspondence problem in the Ternus display; “element motion” and “group motion.” The solution to the correspondence problem is illustrated by the dotted lines.

explanation of Ternus motion, for example the pattern persistence theory by Breitmeyer and Ritter (1986a), in which Ternus motion is mainly determined by the existence of—or lack of—transients from one frame to the other for the central Ternus elements (but see Alais & Lorenceau, 2002; Kramer & Rudd, 1999).

On the other hand, if the discs of the Ternus display differ in their features—for example as illustrated in Figure 3A (upper panel) where the second and the third disc in the first frame (B and C) and the first and the second disc in the second frame (B and C) are different from the other disc and match in luminance and color—participants perceive up to 60% less group motion than in an unbiased display, in which all the discs have the same color and luminance, showing a strong influence of features on correspondence (Hein & Moore, 2012). This strong feature effect is in contrast to the weak or absent influence of features in other ambiguous motion displays (Navon, 1976).

One difference between the Ternus display and other motion displays that have been traditionally used in correspondence research, like the motion quartet, is that in traditional displays the feature influence has to be effective over longer distances, whereas in the Ternus display, the feature influence does not have to span any distance as the relevant central discs are at the exact same spatial position (Figure 3). In the current study we wanted to see if the distance over which the feature information has to act is a critical factor that distinguishes studies that do and those that do not show feature influences. We therefore wanted to examine if the strong feature bias in the Ternus display is distance-dependent. To measure the spatial extent of the feature bias effect, we varied the horizontal offset between the two sets of discs in a modified version of

the Ternus display, so that they would move sideways as well as up and down (Figure 4).

In addition, we wanted to know if the relevant distance over which features had an influence was set in terms of retinotopic or spatiotopic coordinates. In early visual areas information is encoded in a retinotopic frame of reference. But there must also be a mechanism that allows for a nonretinotopic representation, as we perceive the world as stable despite changes in retinal position every time we make an eye movement. That is, the information is remapped in some way to enable a stable perception of our world (Duhamel, Colby, & Goldberg, 1992; Sommer & Wurtz, 2004; Cavanagh, Hunt, Afraz, & Rolfs, 2010).

The question is whether this remapping process happens before or after correspondence has been established. We know that apparent motion is seen in spatiotopic coordinates, i.e., apparent motion is seen between locations in space and not locations on the retina (Rock & Ebenholtz, 1962; Szinte & Cavanagh, 2011). For example, apparent motion is perceived between two objects presented successively at different spatial locations, even when the retinal position of these objects did not change (Rock & Ebenholtz, 1962). The experiments here examine whether the effects of features are remapped in the same way. Here, to distinguish between a retinotopic and a spatiotopic frame of reference, participants made horizontal saccades across the Ternus display, such that the two Ternus frames were horizontally offset on the retina, but not in spatiotopic coordinates. The results from the first experiment without eye movements allow us to determine the rate at which the feature bias decreases with increasing offset and thus provide a baseline for what to expect with eye movements when we can compare the effect of offset in spatiotopic and retinotopic coordinates.

We found that the distance over which the feature effect acts is indeed an important factor that influences its strength, suggesting that at least some of the difference between studies is due to this factor. In addition, we found that the relevant distance is spatiotopic, the distance in the world, not on the retina, indicating that feature based correspondence is established after the element locations have been corrected for the effects of eye movements.

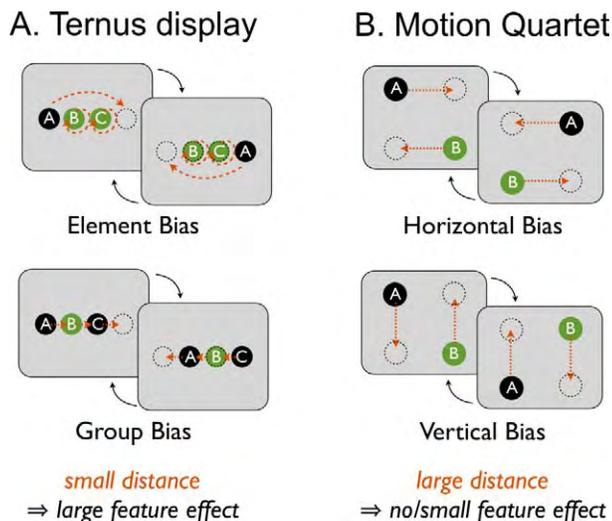


Figure 3. Comparison of two different types of ambiguous apparent motion displays in terms of distance between discs that are connected by feature similarity.

Experiment 1: spatial extent of the feature effect

In order to examine the effect of spatial distance on the feature effect in the Ternus display, we presented the Ternus discs vertically aligned (Petersik, 2009) and introduced different horizontal offsets between the

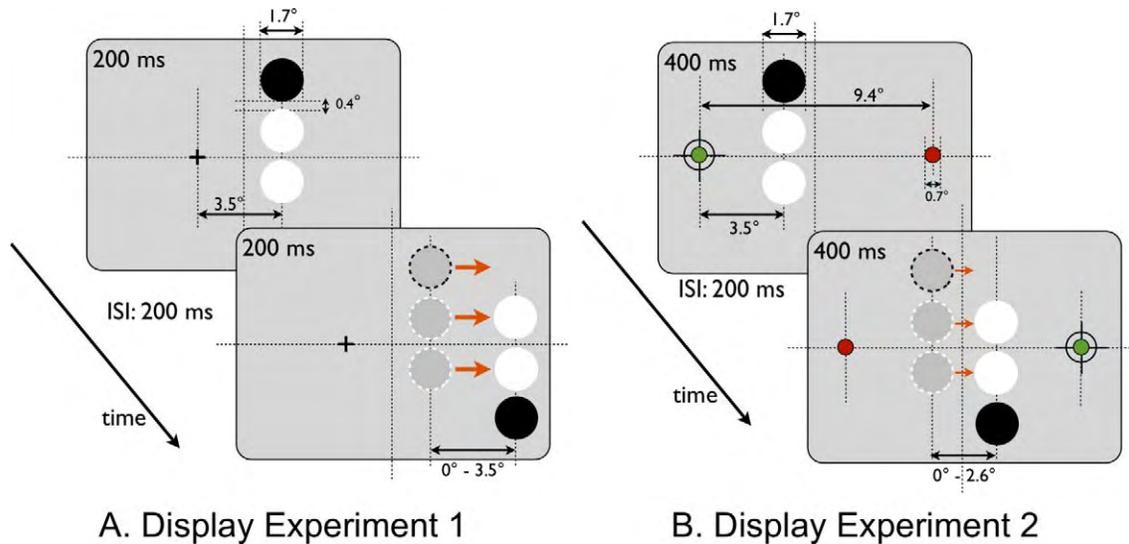


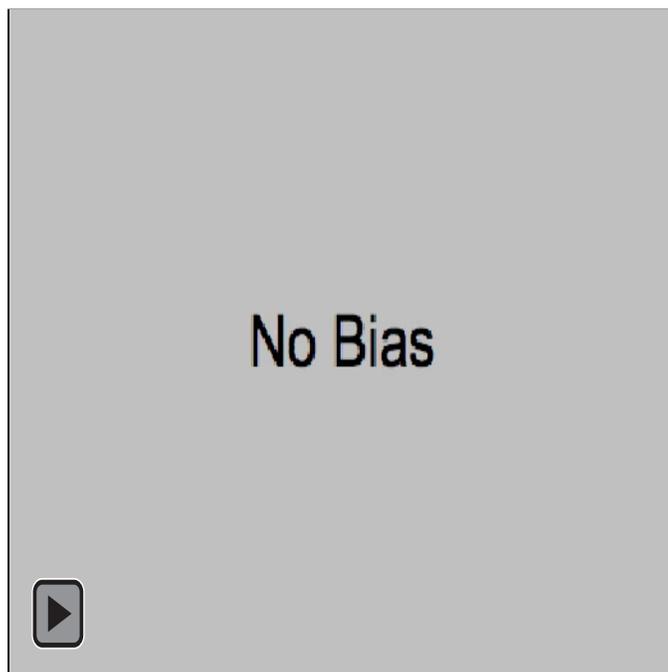
Figure 4. Illustration of the displays used in [Experiment 1](#) (left display, A) and [Experiment 2](#) (right display, B). The dotted circles and orange arrows in frame 2 were used to illustrate the direction of the spatial offset; they were not presented during the experiment.

discs in the first frame and the second frame (Figure 4, left display). We used a constant frame duration and ISI between frames of 200 ms, for which participants usually perceive group motion in the unbiased Ternus display (Kramer & Yantis, 1997).

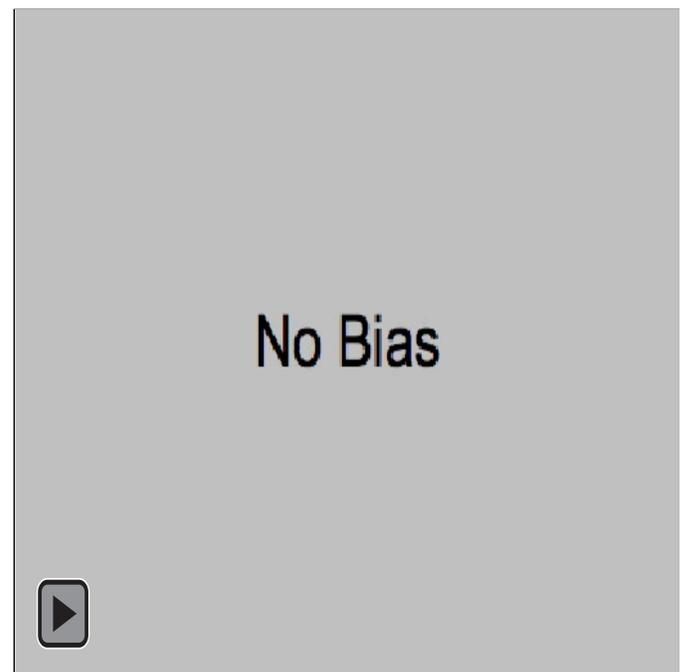
To bias the motion percept towards element motion, we matched the features of the central and lower disc in the first frame and the upper and central disc in the second frame (Movies 1, 2, and 3). We used three

different types of features to bias the motion percept (Figure 5): contrast polarity (black and white discs), size (small and large discs) and changes in “spatial frequency” (outline versus filled-in circles). All these features are known to have an influence on correspondence in the Ternus display (Casco 1990; Dawson et al., 1994).

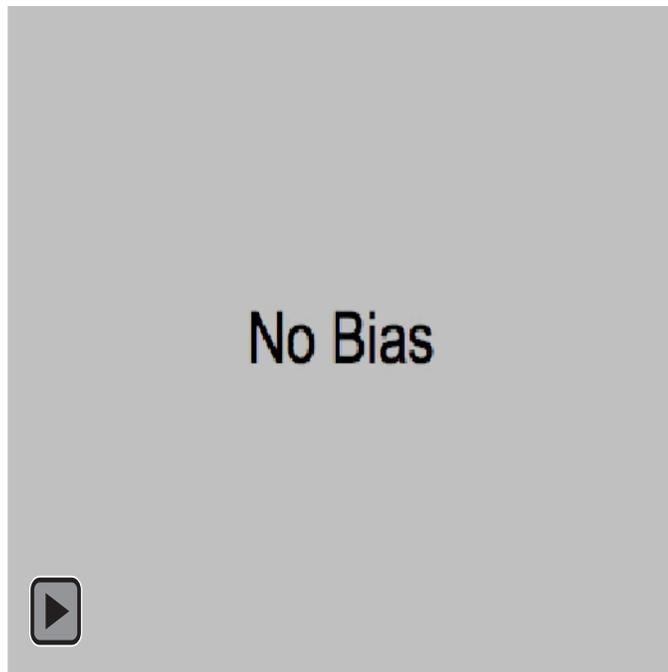
We expected the feature effect to decrease with increasing offset between the two sets of discs.



Movie 1. Illustration of the displays used in [Experiment 1](#) (zero offset condition, no bias and polarity bias). Please fixate the cross at the left.



Movie 2. Illustration of the displays used in [Experiment 1](#) (1.7° offset condition, no bias and polarity bias). Please fixate the cross at the left.



Movie 3. Illustration of the displays used in [Experiment 1](#) (3.5° offset condition, no bias and polarity bias). Please fixate the cross at the left.

Furthermore, we hypothesized on the basis of differences in the size of the feature effect for different features (Hein & Moore, 2012) that the strength with which different features are able to determine correspondence might vary, allowing the feature effect to be effective over larger distances for some features.

Method

Participants

Ten observers participated in this experiment. Six participants were students of Paris Descartes, who were inexperienced and naïve as to the purpose of the experiment and who participated in fulfillment of a course requirement. The other four participants were experienced psychophysical observers from the lab. All reported normal or corrected-to-normal visual acuity and color vision. All participants gave their informed consent before participating.

Apparatus

The experiment was controlled by a Mac Pro 1.1 driving a 22-inch color CRT monitor (Formac ProNiton 22800) with a spatial resolution of 1056×792 and a refresh rate of 140 Hz, using MATLAB software (version 7.5, Mathworks, Natick, MA) with the Psychophysics toolbox extensions (Brainard, 1997;

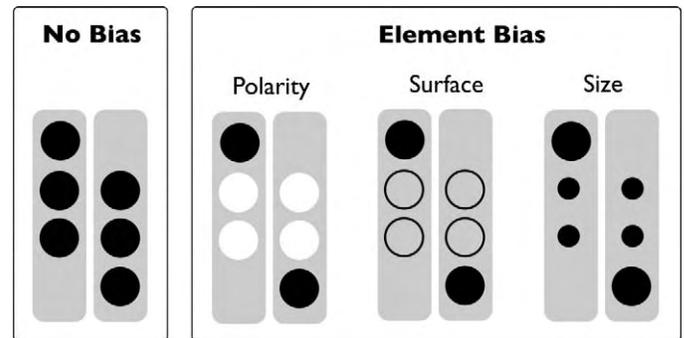


Figure 5. Illustration of the different types of features used to bias the motion percept of the Ternus display towards element motion.

Pelli, 1997). Viewing distance was fixed at 63 cm using a head- and chinrest.

Stimuli

[Figure 4](#) (left display) illustrates the arrangement of the stimuli used in [Experiment 1](#). A fixation cross was presented 1.7° to the left of the center of the display. The Ternus display consisted of two sets of three vertically aligned discs, separated by gaps of 0.4°. Each disc had a diameter of 1.7°. In the first frame the set of discs was horizontally displaced by 3.5° to the right of fixation (measured from fixation to disc center), the center of the lower two discs being horizontally aligned with fixation. The discs in the second frame were vertically moved downwards by one position and presented either at the exact same horizontal position as the first set (0° offset) or horizontally displaced to the right (away from fixation) by 0.2, 0.4, 0.9, 1.7, 2.6, or 3.5° (measured from disc center to disc center). In the no bias condition all discs were black (1.0 cd/m^2) on a gray background (9.5 cd/m^2). In the element bias condition, the lower two elements in the first frame and the upper two elements in the second frame were different from the first and the last element: In the polarity bias condition they were white (26 cd/m^2); in the spatial frequency bias condition, they were empty circles (with a line width of 0.2°); and in the size bias condition, they were smaller discs (diameter of 1.1°).

Task

On each trial, participants made a 2-alternative forced choice (AFC) decision indicating if they perceived all elements as moving up and down (or diagonally, in the case of a horizontal offset) together as a group (*group motion*) or if one of the elements appeared to move separately from the other two, jumping from top to bottom across the other two discs (*element motion*), while the other two discs were either stationary or moved horizontally. Participants pressed the ‘j’ or ‘f’ key

on a standard computer keyboard to indicate that they perceived group or element motion respectively.

Procedure

Each session began with a set of written instructions that included two demonstrations of group motion and two illustrations of element motion (one with no bias and one with a polarity based element bias). After a block of 14 practice trials participants completed 10 experimental blocks of 28 trials each.

Each trial began with the presentation of the fixation cross for 700 ms, followed by the first set of three discs for 200 ms. After an ISI of 200 ms, the second set of three discs appeared for another 200 ms, followed by the same ISI. The display continued to cycle until a response was recorded. The next trial started after a blank screen was presented for 500 ms. If another key than the two possible response keys was pressed, an error message was presented for 1000 ms.

Design

A 4 (Type of Element Bias: No bias, polarity based element bias, spatial frequency based element bias, size based element bias) \times 7 (Horizontal Offset: 0, 0.2, 0.4, 0.9, 1.7, 2.6, or 3.5°) within subjects design was used. All factors were fully crossed and randomly mixed within blocks of trials, resulting in 10 observations in each condition.

Results and discussion

Figure 6 shows the feature bias, i.e., the difference in mean percent of element motion responses between the no bias condition and each of the three element bias conditions, as a function of horizontal offset (in degree of visual angle) for Experiment 1. As can be seen in the figure, the biasing effect of the features in favor of element motion is very strong for each of the three bias conditions in the first four offset conditions with horizontal offsets of less than 1°. This result replicates earlier findings that features can strongly bias correspondence in the Ternus display, even in ISI conditions in which one usually perceives group motion in an unbiased Ternus display (Casco 1990; Dawson et al., 1994; Hein & Moore, 2012). In addition, the strength of the feature bias, favoring element motion, decreased as the horizontal offset between the two Ternus frames increased.

The difference in mean group responses between the no bias condition and the element bias conditions for individual observers were submitted to a two-way analysis of variance (ANOVA) with the factors Type of Element Bias and Horizontal Offset. These analyses

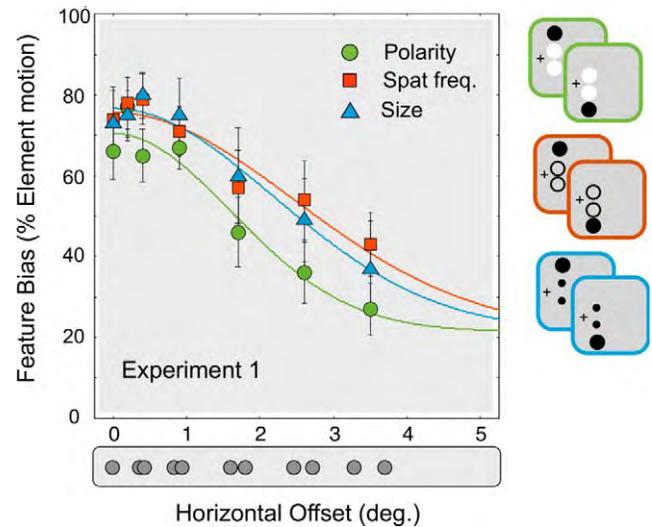


Figure 6. Feature bias (difference in % element motion responses between the element bias condition and the no bias condition) as a function of distance between the discs in the first and the second frame for each of the three types of bias (contrast polarity, spatial frequency, and size). Lines indicate the best-fitting Gaussians. Error bars represent the standard error of the mean in each condition.

confirmed a main effect of Horizontal Offset, $F(6, 48) = 11.43$, $p < 0.001$ and a trend for the factor Type of Element Bias, $F(2, 16) = 3.15$, $p = 0.070$. The interaction between the two factors was not significant, $F(12, 96) = 0.5$. Least significant difference (LSD) post-hoc comparisons for the factor Horizontal Offset revealed significant differences between the three largest offset conditions (1.7°–3.5°) with all of the smaller offset conditions (0°–0.9°). Moreover, the difference between the polarity bias and spatial frequency bias was significant, suggesting that polarity is the weakest feature to influence correspondence.

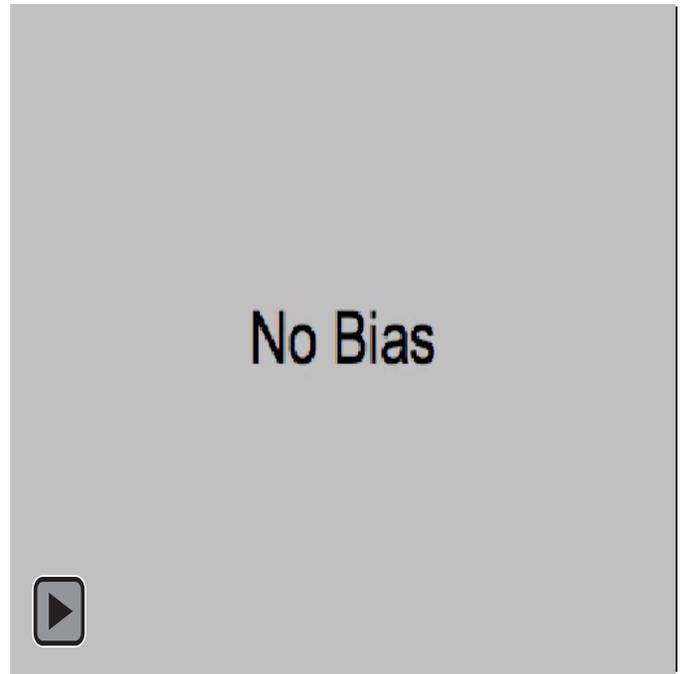
We also fit Gaussian functions to these data. We restricted the fit to positive values with the maximum value at 0, meaning we basically used a half Gaussian, as our data set was unidirectional. The standard deviation (σ) and the maximum values of the fits were free parameters, but we set the minimum of the fit to the feature bias value we found with very large offsets (9.4°–12°) in the fixation condition of an addition to Experiment 2 (21%). We used the standard deviation of the Gaussian fit as an indicator of the critical spacing. It was 2.3° ($SE \pm 0.22$, $r^2 = 0.95$) for the polarity bias and somewhat larger for the size bias (3.1°; $SE \pm 0.17$, $r^2 = 0.97$) and the spatial frequency bias (3.5°; $SE \pm 0.28$, $r^2 = 0.93$). However, since the difference between the three features was not significant, we also fit a Gaussian to the average of all three conditions and found the critical spacing to be 2.9° ($SE \pm 0.17$, $r^2 = 0.97$).

To summarize, we found that features can strongly bias motion perception toward the element organization in the Ternus display. This feature effect was maximum when the offset was smaller than the size of a disc and dropped to 36.8% of this maximum ($1/e$) at about 3.9° horizontal offset. This effect is not likely due to differences in retinal eccentricity with the different offsets as it has been shown that eccentricity has no effect on the appearance of the Ternus display for displays similar to those we used here: Ternus oriented vertically and displaced horizontally away from fixation (Aydin, Herzog, & Ögmen, 2011; Petersik, 2009); in addition, eccentricity effects seem to be more pronounced with smaller stimulus sizes than used here (Breitmeyer & Ritter, 1986b; but see Rutherford, 2003).

Experiment 2: reference frame of the feature effect

Experiment 1 showed that the feature effect in the Ternus display depends on the distance between the two Ternus frames: the larger the offset, the smaller the feature effect. The aim of **Experiment 2** was to examine if this feature effect operates in retinotopic or spatiotopic coordinates. To distinguish between the two, participants had to make horizontal saccades of 9.4° across the Ternus display such that the two Ternus frames were horizontally offset on the retina, but not in spatiotopic coordinates (for the 0° offset condition, see **Movie 4**). **Figure 7** illustrates this difference.

From **Experiment 1** we know that the larger the offset, the smaller the feature effect. Thus, in the 0-offset condition, if the relevant distance for the feature bias would be retinotopic, one would expect a large decrease in the strength of the feature effect in the saccade condition compared to the fixation control condition (**Figure 8**, solid black versus red curve), as there is a large horizontal offset in terms of retinal coordinates (**Figure 7B**). If, on the other hand, the feature bias occurs in spatiotopic coordinates, no difference between the fixation control and the eye movement conditions should be found (**Figure 8**, solid black versus blue curve), because due to the remapping process, i.e., the compensation of the saccades, the horizontal offset is small in both conditions (**Figure 7C**). In order to examine possible interactions between the saccades and the movement of the Ternus display, we also compared two different saccade conditions, one in the direction of the horizontal offset of the Ternus display (saccade with Ternus offset) and one in the opposite direction (saccade against Ternus offset).



Movie 4. Illustration of the displays used in **Experiment 1** (zero offset condition, no bias and polarity bias). Please follow the green disc with your eyes, making saccades between the left and the right side of the display.

Method

Participants

Six experienced psychophysical observers participated in **Experiment 2**, one of them being one of the authors (EH). Some of them also participated in **Experiment 1**.

Apparatus

Computer and software are the same as in **Experiment 1**.

Stimuli

The displays were very similar to **Experiment 1** as illustrated in **Figure 4B**. The first set of Ternus discs was presented 1.3° to the left of the center of the monitor; the second set of Ternus discs was either presented at the same location or 0.9, 1.7, or 2.6° shifted to the right. In addition to the Ternus display, two fixation discs with a diameter of 0.7° were presented 4.7° to the left and the right of the center of the screen. The discs were either red or green and similar in salience.

Task

In the fixation condition, the task was identical to **Experiment 1**. In the saccade conditions, participants had to move their eyes following the green disc.

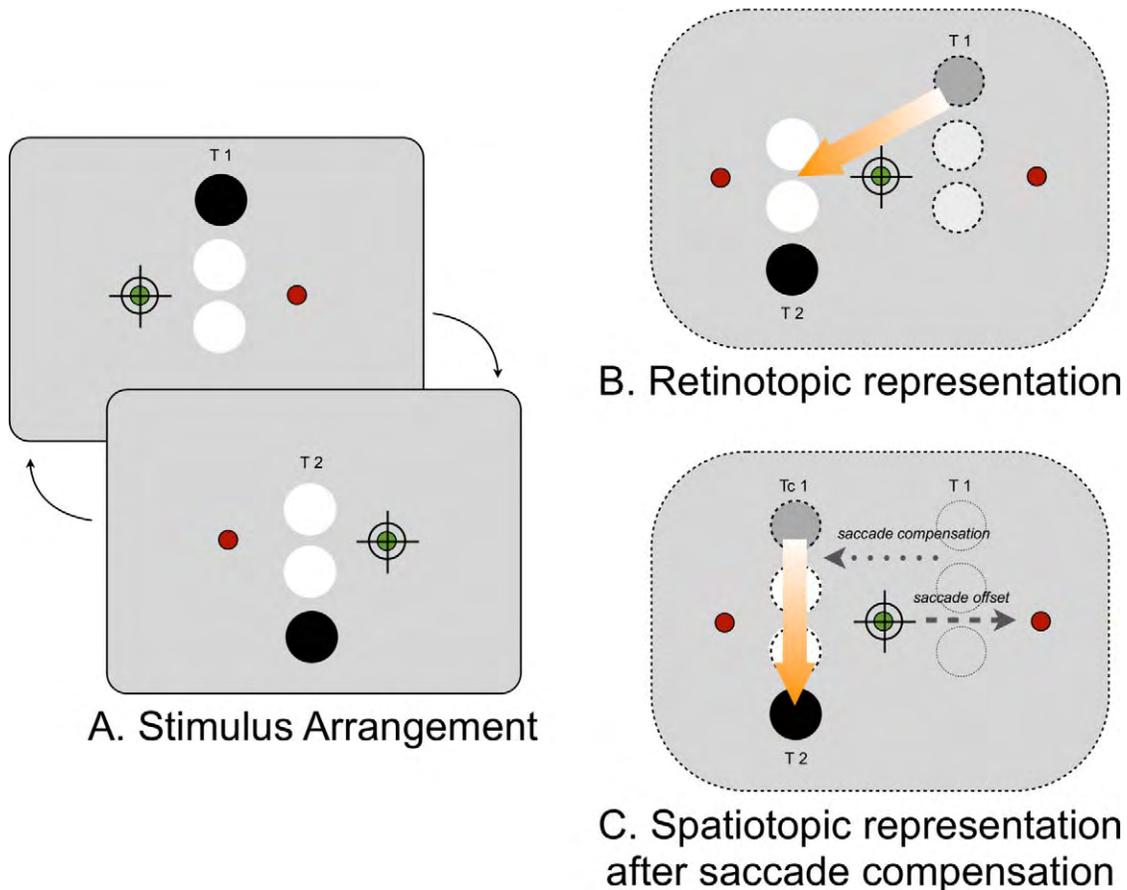


Figure 7. Offsets in Ternus display in spatiotopic and retinotopic reference frames for the 0° spatial offset condition. (A) The stimulus arrangement on the monitor for the first (T1) and the second (T2) Ternus frame; the crosshair represents the position of the eye. (B) T1 and T2 in a retinotopic frame of reference; at the level of the retinal representation the position of T1 discs is always to the right of the fovea. That way, when the fovea moves due to the eye movement, the retinal position of the T1 discs changes as well, resulting in a large horizontal offset between T1 and T2. (C) In a spatiotopic frame of reference, the perceived position of the discs of frame 1 stays the same, as the effect of the saccade is compensated (gray arrows), resulting in no perceived horizontal offset between the two set of discs (Tc1 and T2). The orange arrows represent the direction of apparent motion that one would perceive in the two cases (retinotopic vs. spatiotopic representation).

Procedure

The procedure was similar to [Experiment 1](#). Participants completed 15 experimental blocks of 16 trials each. The different saccade conditions were blocked, and before each set of experimental blocks, participants completed eight practice trials.

The trial sequence is illustrated in [Figure 9](#). Each trial began with the presentation of the two saccade discs, which guided participants' eye movements, the left disc being green, the right disc being red. After 600 ms the two discs switched color, and after another 600 ms, colors switched back again. This initial sequence allowed participants to find the right rhythm for their eye movements. Then the two saccade discs switched colors again, the left one being green and the right one being red. After 100 ms, the first set of Ternus discs was presented for 400 ms. Then the saccade discs were

presented alone for 100 ms before they switched color. After another 100 ms the second set of Ternus discs was presented for 400 ms, followed by the saccade discs alone for 100 ms, before they switched color again. The display continued to cycle until a response was recorded. The next trial started after 1200 ms, unless an error message was presented for 1000 ms when a different key than one of the two response keys was pressed.

Design

A 2 (Element Bias: No bias, polarity based element bias) \times 3 (Saccade condition: Fixation, saccade in the same direction as the Ternus offset, saccade in the opposite direction as the Ternus offset) \times 4 (Horizontal Offset: 0, 0.9, 1.7, or 2.6°) within subjects design was

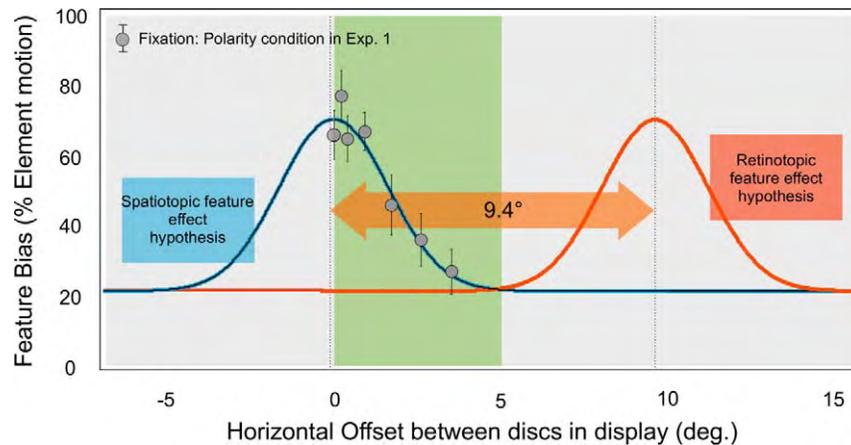


Figure 8. Hypothetical results for Experiment 2, illustrating the feature bias as a function of Horizontal Offset spanning from -7 to $+15$ degrees of visual angle. We consider three different conditions: (1) Fixation (solid black line; data points from the polarity condition in Experiment 1), (2) Feature effect in a spatiotopic reference frame (blue line), and (3) Feature effect in a retinotopic reference frame (red line). Thus in a spatiotopic reference frame, one would expect no difference between the fixation and the saccade condition, as the perceived horizontal offset should be the same in both conditions. In a retinotopic reference frame, however, there would be a very large difference between the fixation and the saccade condition as the shift due to the horizontal saccade of 9.4° has to be added in the saccade condition. The green area represents the range of horizontal offset that we used in Experiment 1.

used. The factors Element Bias and Horizontal Offset were fully crossed and randomly mixed within blocks of trials; the factor Saccade Condition was blocked. Ten observations in each condition were collected.

Results and discussion

Figure 10 shows the feature bias, i.e., the difference in mean percent of element motion responses between the mean of all the no bias conditions and each of the

element bias conditions, as a function of Horizontal Offset (in degree of visual angle) for two saccade conditions (fixation, saccade; we collapsed the data across the two saccade conditions, saccade with Ternus offset and saccade against Ternus offset, as there was no significant difference between them). As illustrated in the graph, we found a very strong feature bias in the 0° offset condition, replicating Experiment 1. Furthermore, this feature effect was very similar with and without saccades (73% in the fixation condition and 67% in the saccade conditions with 0° offset on the display). This is strong evidence that the feature

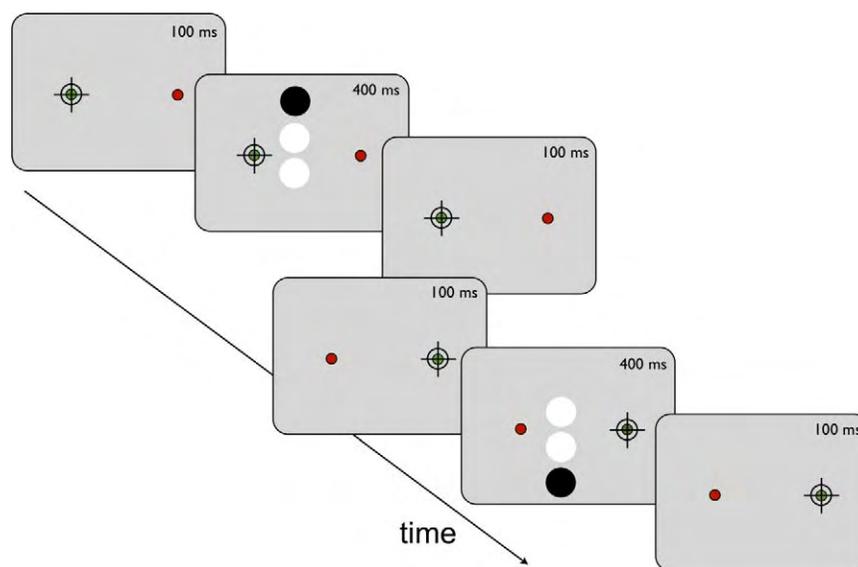


Figure 9. Trial sequence in Experiment 2 (example of a 0° offset condition with feature bias). Participants were asked to follow the green fixation disc with their eyes while they observed the Ternus display and indicated if they perceived element or group motion.

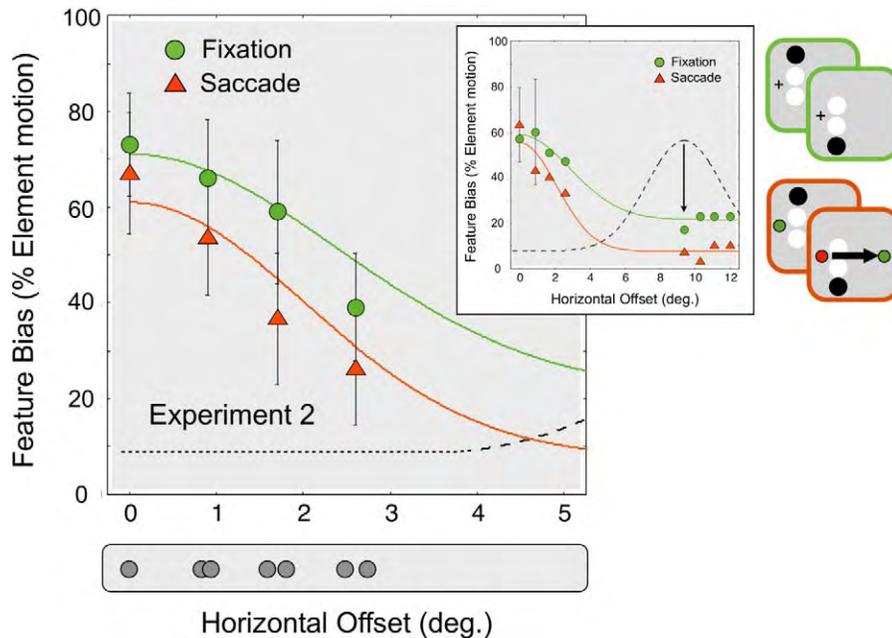


Figure 10. Feature bias (difference in % element motion responses between the element bias condition and the no bias condition) as a function of distance between the discs in the first and the second frame for fixation and saccade condition. Lines indicate the best fitting Gaussian. The dashed black line represents the beginning of the feature effect that would have been expected under the retinotopic feature effect hypothesis (peaking further to the right as can be seen in the inset). Error bars represent the standard error of the mean in each condition. The inset shows data when especially large offset conditions are included ($N = 3$) that extend to the retinotopic locations the Ternus elements had before the saccade (the vertical arrow at 9.4° indicates the point of minimum retinotopic offset, i.e., retinotopic match between the discs in frame 1 and 2). The dashed black line represents again the retinotopic feature effect hypothesis. The error bars are shown only for one representative point in the saccade and fixation conditions.

influence happens in spatial coordinates and not in retinal coordinates, as the 0° offset condition has a large offset in retinal coordinates, about 9° , which, from the data in Figure 6 for Experiment 1, should have produced a much smaller feature effect (Figure 8).

The differences in mean percent of element responses between the average of the no bias condition in all three saccade conditions and the element bias conditions for individual observers were submitted to a two-factor ANOVA with the factors Saccade Condition and Horizontal Offset. For the factor Saccade Condition we collapsed the data across the two different saccade conditions (saccade with Ternus offset and saccade against Ternus offset), as previous analysis indicated that there was no significant difference between them. These analyses confirmed a main effect for Horizontal Offset, $F(3, 15) = 3.33$, $p < 0.05$, as the strength of the element bias decreased from 70% at the 0° offset condition to 32% at the highest offset condition. Furthermore, the average element bias across the four offsets decreased significantly from 59% in the fixation condition to 45% in the saccade condition, as confirmed by a main effect for the factor Saccade Condition, $F(1, 5) = 10.10$, $p < 0.05$. The interaction between the two factors was not significant, $F(3, 15) = 1.20$, which suggests that the

feature bias is not retinotopic, as the difference between the fixation and the saccade conditions should have been much larger for the 0° offset condition than for the larger offset conditions under the retinotopic feature effect hypothesis. The significant decrease in the size of the element bias in the saccade condition might be due to the fact that in the saccade condition participants had to judge the Ternus motion while executing eye movements at the same time. Aydin et al. (2011) showed that the Ternus motion is affected by reducing attention to the Ternus in a dual task paradigm. If attention is important for the feature effect in the Ternus display, it is therefore possible that dividing attention between the Ternus motion and the saccade task reduced the influence of the feature bias in the saccade condition.

Gaussians were again fitted to the data, one to the saccade and one to the fixation condition. In the fit, we restricted the maximum of the Gaussian to positive values, as our data are unidirectional, but allowed horizontal shifts of the maximum of the curve, in order to test for our hypothesis of a potential shift in the direction of the saccade if correspondence was solved in a retinotopic frame of reference. In addition, we fixed the lowest value of the fit to 21.4% and 7.6% for the fixation and saccade conditions, respectively, as these

were the lowest values that we found with very large offsets (see below). The critical spacing (σ of the Gaussian) in the fixation control condition was 3.4° ($SE \pm 0.18$, $r^2 = 0.99$), and 2.9° ($SE \pm 0.62$, $r^2 = 0.85$) in the saccade condition. Thus, the critical spacings in the fixation control condition and the saccade condition were not significantly different from each other. More importantly, the fit in both cases showed no evidence for a shift in the feature bias effect toward the 9.4° center (Figure 8) that would be predicted if the feature bias were based on retinotopic distance.

Saccades tend to undershoot the target position by about 10% (Becker, 1972). It is possible that these errors in the saccade landing position could have introduced an error of the remembered presaccadic location of the stimuli in the first Ternus frame, which might have increased the perceived stimulus offset of the second Ternus frame. Previous studies, however, have found that the judgments of probe positions are independent of saccade landing positions (Collins, Rolfs, Deubel, & Cavanagh, 2009). Furthermore, Szinte and Cavanagh (2011) showed for saccades very similar to those performed in our experiment that the position judgment of the presaccadic stimulus is independent of the saccade landing position on a trial-by-trial basis. These studies suggest that the visual system compensates for errors in the saccade landing location. As a consequence, these errors should not affect the perceived pre-saccadic position of the stimuli, and thus it is unlikely that errors in the saccade landing position affected the perceived offset of the second Ternus frame in this study.

We found a very similar decrease of the feature bias in both the fixation and the saccade conditions, suggesting that the feature bias effect is acting in a spatiotopic reference frame. There is, however, the possibility that the feature bias effect could be effective in both spatiotopic and retinotopic coordinates. We tested this in an additional experiment in which we presented, together with the four offsets used in Experiment 2, four new offsets that were retinotopically matched to the presaccadic locations of the Ternus elements. We did this by adding the size of the saccade to the original offsets (9.4° ; 10.3° ; 11.1° ; 12°). As the inset of Figure 10 illustrates, there is no evidence for an additional retinotopic peak in the feature bias. We again fitted Gaussians to the data, restricting as before the maximum of the Gaussian to positive values, but now allowing the lowest value of the Gaussian to vary. The critical spacing (σ of the Gaussian) in the fixation control condition was 4.0° ($SE \pm 0.68$, $r^2 = 0.98$) and 2.9° ($SE \pm 3.0$, $r^2 = 0.53$) in the saccade condition. The lowest values of the fits here (21.4% and 7.6% for the fixation and saccade conditions, respectively) appear to represent a stable minimum that shows no further decrease, even 2.6° beyond the location of the

retinotopic match. We used these minimum values in the previous Gaussian fits (Experiment 1 and Experiment 2, main condition).

To summarize the results of Experiment 2, we found that the spatial range of the feature bias is similar whether an eye movement has occurred between the two Ternus frames or not. It is centered at the display location of the stimuli on the first frame and the critical spacing in both conditions is very similar. These results suggest that the feature bias is set in spatial coordinates.

General discussion

Several studies now clearly show that when determining the identity of an object across changes in location, the visual system does make use of feature information (Casco 1990; Dawson et al., 1994; Hein & Moore, 2012; Kramer & Rudd, 1999; Kramer & Yantis, 1997; Petersik & Rice, 2008). Here we showed that this feature effect is especially strong in the traditional Ternus display, when some of the matching discs are at the same position, and it becomes less strong the larger the offset between these discs becomes (apparently without ever disappearing completely, however). This spatially dependent feature effect could explain why the Ternus display shows an especially strong feature effect, while other ambiguous motion displays, such as the motion quartet, do not. Furthermore, our second experiment showed that the range of the feature effect is set in spatial coordinates and not in retinal coordinates.

Our findings provide further support for a growing body of studies that show the importance of feature information for resolving the correspondence problem, not only in apparent motion, but also in other domains including visual working memory, attention, the guidance of eye movements, and the establishment and maintenance of object representations (Hollingworth & Franconeri, 2009; Hollingworth, Richard, & Luck, 2008; Hollingworth & Rasmusen, 2010; Moore, Stephens, & Hein, 2010; Richard, Luck, & Hollingworth, 2008; Tas, Dodd, & Hollingworth, 2012). Together these findings strongly question the spatiotemporal priority hypothesis (Flombaum, Scholl, & Santos, 2009; Scholl, 2001) that suggests that only spatiotemporal factors are important for determining correspondence.

The finding that the feature effect uses a spatiotopic frame of reference (Experiment 2) challenges theories that suggest that short range motion detectors determine the element motion percept of the Ternus display (Petersik & Pantle, 1979) and more generally motion correspondence (Nishida & Takeuchi, 1990). In the

saccade condition we introduced shifts in retinal distance between successive Ternus disc frames that were too large to be processed by short-range motion detectors, but found nevertheless a strong bias towards element motion. We do not want to suggest that short range motion detectors can never play a role in determining motion correspondence, but at least our findings suggest that there is another kind of mechanism that the visual system can use to determine correspondence (and leading to either the percept of element motion or the percept of group motion in the Ternus display). We propose that this higher-level mechanism determines correspondence depending on feature similarity and assigns motion based on which elements belong together, instead of computing motion energy and in a second step correspondence based on motion (see also Ögmen, 2007).

A possible mechanism that would be able to do this kind of attribution could be an attention-based motion system as proposed by Cavanagh (1992), in which attentional pointers that operate on feature information provide information about displacements in space. Our findings suggest that these pointers might work in a spatiotopic frame of reference, which is in line with a recent proposal by Cavanagh and colleagues that attentional pointers could be the basis of remapping (Cavanagh et al., 2010). The importance of attention in nonretinotopic processing can be also seen in recent studies of feature integration, visual search, and apparent motion in a nonretinotopic frame of reference (Cavanagh, Holcombe, & Chou, 2008; Boi, Ögmen, Krümmenacher, Otto, & Herzog, 2009; Ögmen, Otto, & Herzog, 2006; Otto, Ögmen, & Herzog, 2008; see also Aydın et al., 2011, for effects of attention on Ternus motion).

In sum, we found evidence that the visual system calls on feature information when solving the correspondence problem, in particular, when there is only a small offset between the two locations to be matched. The critical offset is set in spatial coordinates suggesting that the output of simple, retinotopically based motion detectors cannot be contributing to this aspect of the correspondence problem.

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