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Spatio-Temporal Priority Revisited: The Role of Feature Identity and Similarity for Object Correspondence in Apparent Motion

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Abstract

We live in a dynamic environment in which objects change location over time. To maintain stable object representations the visual system must determine how newly sampled information relates to existing object representations, the *correspondence problem*. Spatiotemporal information is clearly an important factor that the visual system takes into account when solving the correspondence problem, but is feature information irrelevant as some theories suggest? The Ternus display provides a context in which to investigate solutions to the correspondence problem. Two sets of three horizontally aligned disks, shifted by one position, were presented in alternation. Depending on how correspondence is resolved, these displays are perceived either as one disk “jumping” from one end of the row to the other (*element motion*) or as a set of three disks shifting back and forth together (*group motion*). We manipulated a feature (e.g., color) of the disks such that, if features were taken into account by the correspondence process, it would bias the resolution of correspondence toward one version or the other. Features determined correspondence, whether they were luminance-defined or not. Moreover, correspondence could be established on the basis of similarity, when features were not identical between alternations. Finally, the stronger the feature information supported a certain correspondence solution the more it dominated spatiotemporal information.

Keywords

apparent motion; object updating; correspondence problem; spatio-temporal priority

Visual perception requires the organization of the retinal image into meaningful units that reflect objects in the world. It also requires that representations of those objects be updated over time. The ambiguity of the visual input makes this a nontrivial problem. Imagine that you are in a crowded mall trying to follow your friend from a distance. You can do this despite the fact that your friend disappears and reappears as he/she moves from one store to

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the next and behind other people and objects. To do this some set of visual processes must determine which parts of a given retinal image at a given time belong to the critical object (in this case your friend) and which do not.

This problem—which following Ullman (1979) we refer to as the *correspondence problem*—has important consequences regarding how we perceive the world around us. If correspondence is established between two stimuli that appear at different times, then the object representation that was established by the first stimulus will be updated (i.e., altered) to reflect the more recent information contained in the later stimulus. In contrast, if correspondence is not established between those two stimuli, then a distinct object representation must be created to represent the more recent information contained in the later stimulus. The difference between having established correspondence or not, therefore, can mean the difference between perceiving one or two objects (see Moore & Enns, 2004; Moore, Mordkoff, & Enns, 2007) or the difference between keeping track of an already established object versus failing to do so (think about your friend at the mall).

Given the importance of correspondence in perception, the basis on which visual correspondence is established has received considerable attention over the years. The evidence remains mixed, however, with regard to the relative importance of feature information (e.g., color, luminance, texture, shape) in establishing object correspondence compared with the importance of simple proximity of stimuli in space and time, or what has been referred to collectively as *spatiotemporal* information (see Figure 1).

The early literature focused on understanding correspondence in the context of apparent motion in particular (Kolars & Pomerantz, 1971; Ullman, 1979). Some of these studies used displays that were unambiguous with regard to correspondence in that there was only a single stimulus at the two different time points (e.g., Cavanagh, Arguin, & von Grünau, 1989; Kolars & Pomerantz, 1971). These asked which variables affected the quality of motion perceived. Other studies used displays that were ambiguous with regard to correspondence, and depending on how it was resolved one or another motion percept was experienced (e.g., Burt & Sperling, 1981; Navon, 1976; Ullman, 1979). These studies asked which variables could bias perception toward one percept or the other. Both spatiotemporal variables, such as the distance and time between stimuli, and feature variables, such as color and shape, were assessed in these studies. Generally, spatiotemporal factors tended to dominate the correspondence processes in apparent motion, with other features playing rather a minor role (e.g., Burt & Sperling, 1981; Kolars & von Grünau, 1976; Kolars & Pomerantz, 1971; Navon, 1976; Nishida & Takeuchi, 1990; Nishida, Ohtani, & Ejima, 1992; Werkhoven, Sperling, & Chubb, 1993, 1994; but see, for example, Green, 1986, 1989; Sekuler & Bennett, 1996; Shechter, Hochstein, & Hillman, 1988).

The introduction of the object-file framework by Kahneman, Treisman, and Gibbs (1992) raised the idea of object correspondence, in particular, as distinct from motion correspondence.¹ This framework states that object representations (*object files*) are defined

¹Although perceived motion intuitively implies a single object, in fact, the perception of motion is separable from the perception of form (e.g., Adelson & Bergen, 1985), and in principle, one could perceive motion between two stimuli and still perceive two objects.

on the basis of spatiotemporal factors, without regard to other features (see also, Pylyshyn, 2000). Feature information is not integrated into object representations as attributes of the object until after correspondence is established. It follows within this theoretical framework, therefore, that feature information cannot play a role in the definition of object representations themselves. Consistent with this prediction, using the object-reviewing paradigm that was originally introduced by Kahneman et al. (1992) to measure the establishment of object files, Mitroff and Alvarez (2007) found object-specific preview benefits when there was a smooth spatiotemporal path relating the previewed stimulus to the test stimulus. However, when only color, size, topology, and/or luminance related the two stimuli there were no object-specific preview benefits. These observations are exactly what would be expected if object correspondence required spatiotemporal coherence, and if the features of the stimuli played no role in that process (but see Moore, Stephens, & Hein, 2010).

Studies of multiple object tracking have also led to the proposal that features play no role in object correspondence (Pylyshyn & Storm, 1988; Pylyshyn, 2004). Consistent with the assertion, people can track up to about five identical independently moving objects, indicating that feature distinctions are not necessary for object individuation. Moreover, when object features do change, participants are unable to report their identity, suggesting that the features themselves were not included in the representations of the tracked objects (e.g., Horowitz et al., 2007).

Although the evidence reviewed so far seems to favor spatiotemporal priority (Flombaum, Scholl, & Santos, 2009) of correspondence processes, other evidence complicates the picture. Using the same object-reviewing paradigm as Mitroff and Alvarez (2007), Moore, Stephens, and Hein (2010) found that abruptly changing the features of the continuously moving objects (i.e., ones that possessed spatiotemporal continuity) disrupted the object-specific preview benefit (see also, Hollingworth & Franconeri, 2009). If features play no role in the maintenance of object representations, then changing features should have played no role in the object-specific effects (see also, Moore, Mordkoff, & Enns, 2007).

Returning to apparent motion, feature information has been found to impact not only the quality of perceived motion in simple apparent motion displays, albeit minimally (e.g., Berbaum, Lenel, & Rosenbaum, 1981; Cavanagh, Arguin, & von Grünau, 1989), but also to influence how correspondence is resolved in ambiguous apparent motion displays (e.g., Green, 1986, 1989; Mack, Klein, Hill, & Palumbo, 1989; Sekuler & Bennett, 1996), especially in a display known as the *Ternus* display (Ternus, 1926; Pikler, 1917). In a typical Ternus display, three horizontally aligned disks are presented in a row, followed by the same disks shifted one position to the left or right after a blank frame (see Figure 2). The duration of the blank frame, the *interstimulus interval* (ISI), varies. When ISI is long, participants tend to perceive the disks as moving together as a group (*group motion*), whereas when ISI is short, they tend to perceive one disk “jumping” from one end of the row to the other (*element motion*). Notice that group and element motion imply different resolutions to the correspondence problem in this display. Specifically, A' , B' , and C' , the disks that correspond to disk A, B, and C in Figure 2, is different for element and group motion. Thus, perceived Ternus motion provides a measure of how correspondence was resolved.

Multiple studies have shown large effects of stimulus features on the correspondence process in Ternus displays (Casco, 1990; Dawson, Nevin-Medows & Wright, 1994; Kramer & Rudd, 1999; Kramer & Yantis, 1997; Petersik & Rice, 2008). Kramer and Yantis (1997), for example, manipulated shape so that the first element of the first frame and the last element of the second frame had different shapes from the other two elements in the display. They found that participants tended to perceive more element motion in this condition, compared with a condition in which all the elements had the same shape (see also Casco, 1990). Similar effects have been observed with contrast polarity (Dawson et al., 1994), texture, and color (Petersik & Rice, 2008).

Why do features sometimes have almost no influence on the correspondence process, whereas other times they strongly influence the correspondence process? Ambiguity of the displays cannot account for these differences. Ambiguity is neither necessary nor sufficient for revealing feature effects on correspondence. Feature effects have been observed for both unambiguous apparent motion in which there is only one solution to the correspondence problem (e.g., Cavanagh, Arguin, & von Grünau, 1989; Watson, 1986) and ambiguous motion displays in which there are multiple possible solutions to the correspondence problem (e.g., Casco, 1990; Kramer & Yantis, 1997). At the same time, there are studies that found no evidence of feature effects in unambiguous displays (e.g., Kolers & Pomerantz, 1972) and ambiguous motion displays (e.g., Burt & Sperling, 1981; Navon, 1976; Nishida & Takeuchi, 1990; Ullman, 1979).

Another possible explanation for the mixed findings is that whereas some feature information might be available under some conditions to influence the correspondence process, other feature information under other conditions may not be available at the right time to influence the correspondence process (e.g., Anstis, 1970; Green, 1986; Kolers & Pomerantz, 1971; Navon, 1976; Ramachandran, Ginsburg, & Anstis, 1983). Features vary in the speed with which they are processed within the visual system (Allik & Kreegipuu, 1998; Bartels & Zeki, 2005). They also vary in their relative activation of transient and sustained responses within the visual system (e.g., Breitmeyer & Ganz, 1976). Both of these differences could influence the extent to which feature information is available at the right time to influence correspondence processes.

In summary, the literature on the role of features in correspondence processes is mixed. Despite this, the literature concerned with object representation, in particular, takes for granted the assertion that spatiotemporal factors determine correspondence and that feature information is integrated into those representations only after correspondence is established on the basis of the spatiotemporal information (e.g., Kahneman et al., 1992; Mitroff & Alvarez, 2007; Flombaum, Scholl, & Santos, 2009; Pylyshyn, 1994; Pylyshyn & Storm, 1988; Xu & Carey, 1996; Xu, Carey, Quint, 2004; Yi, Turk-Browne, Flombaum, Kim, Scholl & Chun, 2008).

In the current study we tested the influence of different features on correspondence using Ternus displays (Ternus, 1926; Pikler, 1917) as the test bed because the different perceptions of the Ternus display clearly indicate different resolutions to correspondence and thus different organizations of the displays in terms of the component objects. We asked, in

particular, which features can influence correspondence, whether feature information ever dominates spatiotemporal information with regard to correspondence, and whether different degrees of feature similarity (rather than identity) are sufficient to bias correspondence. Using a strategy similar to that of Petersik and Rice (2008), we manipulated the features of the individual disks in the Ternus display in such a way as to bias either group or element motion (see Figure 3). If features are used to resolve correspondence, then Ternus perception (i.e., the amount of group vs. element motion responses) should reflect the feature bias, whereas if they are not, then Ternus perception should reflect ISI only. An overview of the different stimulus conditions tested is provided in Figure 3.

Method

Participants

Twelve observers participated in each of the eight experiments (mean age 19.25 (range 18–25; 50 female and 46 male). All observers were undergraduates, received course credit for their participation, and provided their informed consent. Nobody participated in more than one experiment, and all were naïve as to the purpose of the experiment. All reported normal or corrected-to-normal visual acuity and normal color vision. Participants who showed no increase or a decrease of group motion responses in the no bias condition as function of ISI were replaced. Based on this criterion, five, four, four, six, zero, three, two, and one participants were replaced in Experiment 1a, Experiment 1b, Experiment 2a, Experiment 2b, Experiment 3, Experiment 4a, Experiment 4b, and Experiment 4c, respectively.

Apparatus

The experiments were controlled by Power Macintosh computers (Mac OS X, Versions 10.4.10) driving a 17-inch color CRT monitor with a spatial resolution of 1024×768 and a refresh rate of 100 Hz, using MATLAB software (version 7.4 release 2007a, Mathworks, MA) with the Psychophysics toolbox extensions (version 3.0.8, flavor beta; Brainard, 1997; Pelli, 1997). Viewing distance was fixed at 64 cm using a chin-and-head rest. All experiments were conducted with regular room lights put on low (39 cd/m^2) in a small room.

Stimuli

The displays consisted of two sets of three disks with a diameter of 1.5° , separated from each other by a gap of 0.5° and a $0.3^\circ \times 0.3^\circ$ fixation cross at the center of the screen. The disks were presented 1.3° above the fixation cross, the two central disks vertically aligned with it, and the third disk either to the left or to the right of it. All stimuli were presented on a gray background with a luminance of 27 cd/m^2 in Experiment 2b and 4C, a luminance of 41 cd/m^2 in Experiment 4a, and a luminance of 63 cd/m^2 in all other experiments. The fixation cross was white (147 cd/m^2) in Experiments 2B and 4C and black in all other Experiments (5 cd/m^2).

The disks' surfaces depended on the experiment. In Experiments 1A and 3 they were either black (5 cd/m^2) or white (147 cd/m^2). In Experiment 1b they were either green (117 cd/m^2) or blue (23 cd/m^2). Experiment 2a used Gabor patterns of two different orientations, tilted 45° to the right or to the left, with a spatial frequency of 4 and an average luminance of 64

cd/m². In Experiment 2b the disks' surface was presented in two different iso-luminant colors, turquoise and red-orange/salmon, both having a luminance of (42 cd/m²). Experiment 4A used white (96 cd/m²) and black (5 cd/m²), as well as a dark gray (24 cd/m²) and a light gray (70 cd/m²). Experiment 4c used five different iso-luminant colors, including the turquoise and the salmon of Experiment 2b, as well as a light gray, olive-green and pink, all having a luminance of (42 cd/m²).

Task

Participants indicated whether they perceived all elements as moving together (group motion) or whether they saw the first element jumping from the left to the right and the other two elements remaining stationary (element motion) by pressing the 'f' or the 'j' key on the computers' keyboard. Participants were instructed to always press a key even when they were not sure about their response.

Procedure

Each session, which lasted approximately 45 minutes, began with a set of written instructions describing the task presented on the computer screen. After reading the instructions, two extreme examples of group and element motion were shown (using a ISI of 0 and 300 ms) and the experimenter repeated the main points and answered any questions. Afterward observers completed 16 practice trials. During the experimental blocks a break was provided every 40 or 48 trials (depending on the experiment). The next block could be initiated at any time by pressing a button on the keyboard.

Trial events are illustrated in Figure 4. Each trial began with the presentation of the fixation cross and the first set of three disks for 200 ms at position 1, followed by a blank screen with the fixation cross only. After a variable ISI of either 0, 20, 40, 80, 120, 160, 200, or 300 ms the second set of three disks appeared for another 200 ms at position 2, followed again by a blank screen displaying only the fixation cross for the same ISI. The display continued to cycle until a response was recorded. An intertrial interval of 1000 ms separated consecutive trials. If participants pressed a key that was not one of the response keys an error message was displayed.

Design

The exact design of the different experiments varied slightly, but they all included eight different interstimulus Intervals (0, 20, 40, 80, 120, 160, 200, or 300 ms) and all but Experiment 3 included three different Motion Bias conditions. As illustrated in Figure 3 in the no bias condition, all disks had the same features. In the element bias conditions the features of the individual disks were biased toward an organization of the disks in terms of element motion, usually the second element in frame one and the first element in frame 2 having either the exact same feature (Experiment 1, Experiment 2, and Experiment 3), similar feature (Experiment 4A and b) or being the single odd element in each frame (Experiment 4c). In the group bias conditions the disks' features are in accordance with the perception of group motion, the second element of the first frame and the second element of the second frame having the same or similar features.

The exact design of the different experiments was as follows: Experiment 1A used a 2 (Position of the Odd Element: left, center) $\times$ 2 (Odd Color: more white; more black) $\times$ 3 (Motion Bias: no bias, element bias, group bias) $\times$ 8 (Interstimulus Interval) within subjects design. Experiments 1B, 2A/B, and 4A/B used a 2 (Odd Color) $\times$ 3 (Motion Bias) $\times$ 8 (Interstimulus Interval) within subjects design. Experiment 3 used a 2 (Odd Color) $\times$ 5 (Degree of Bias: three-element-bias, two-element-bias, ambiguous, two-group-bias, three-group-bias) $\times$ 8 (Interstimulus Interval) within subjects design. Experiment 4C used a 5 (Motion Bias: no bias all gray, group bias 1, element bias 1, group bias 2, element bias 2) $\times$ 8 (Interstimulus Interval) within subjects design. All factors were counterbalanced and randomly mixed within blocks of trials. Data were recorded from a total of 400 trials in Experiment 5 and 480 trials in all other experiments.

Data Analysis

Alpha was set at .05. When appropriate, reported p values were Greenhouse-Geisser corrected. A conservative approach was taken to post hoc comparisons. When a difference between conditions was predicted, we used Scheffé tests, which are relatively conservative with regard to revealing significant differences. When equivalence between conditions was predicted, we used Fisher LSD tests, which are relatively liberal with regard to revealing significant differences.

Experiment 1

Can Luminance-defined Feature Information Influence Correspondence?

The purpose of Experiment 1 was to replicate the finding that luminance cues can determine correspondence in the Ternus display. Experiment 1A used contrast polarity, and Experiment 1B used hue and luminance as cues. In the element bias condition, the second disk in the first frame and the first disk in the second frame were the odd elements, whereas in the group motion condition the odd item was the second disk in both frames (see Figure 3). A baseline measure was provided by a no bias condition in which all the disks in both frames had the same color and luminance, using either black or white (Experiment 1A) and either green or blue (Experiment 1B) for all disks.

Experiment 1A included an additional condition in which the position of the odd element was not the center disk of the first display, but was the left most disk. For the element bias condition, then, the last disk in the second frame was the odd item, whereas in the group motion condition first disk in the second frame was the odd item (see Figure 5).

Results and Discussion

The results confirmed that luminance cues influence correspondence in Ternus displays. Figure 6 shows the mean percent of group motion responses as a function of motion bias and interstimulus interval for Experiment 1A. The left graph shows the condition in which the odd element was on the left, and the right graph shows the condition in which the odd element was in the center position. Because the baseline no-bias condition was the same across the two configuration conditions, we presented the same data in both graphs as reference. In addition we collapsed the data over the odd color condition and all black disks

for the graph as the differences between the two conditions were negligible. Mean group responses for individual observers were submitted to a four-factorial analysis of variance (ANOVA) with the factors Position of the Odd Element (left, center), Odd Color (more white, more black), Motion Bias (no bias, element bias, group bias) and ISI (0, 20, 40, 80, 120, 160, 200, or 300 ms).

There was a reliable main effect of Odd Color $F(1, 11) = 10.44, p < .01$, mean group motion ratings being slightly higher when more of the disks were black (58.13%) than when they were mostly white (55.03%). But this difference was very small, and the factor Odd Color did not interact with any other factor. Consistent with the literature (Pantle & Picciano, 1976; Petersik & Pantle, 1979), group motion ratings increased significantly with increasing ISI (from 25.21% to 69.74%), main effect of ISI, $F(7, 77) = 48.80, p < .001$. Moreover, group motion ratings were lower when the odd item was the leftmost item (52.65%) than when it was the center item of the group (60.51%), as the main effect of the Position of the Odd Element confirms, $F(1, 11) = 17.40, p < .01$. Finally, and most importantly, there was a main effect of Motion Bias, $F(2, 22) = 55.10, p < .001$. As expected, group motion ratings were lowest in the element motion condition (22.36%), higher in the no bias condition (61.84%), and highest in the group motion condition (85.55%). Scheffé post hoc tests revealed that all three motion bias conditions were significantly different from each other. The factor Motion Bias interacted with the factor Position of the Odd Element, $F(2, 22) = 10.51, p < .001$, as well as with the factor ISI, $F(14, 154) = 14.22, p < .001$. In addition, the factors Position of the Odd Element and ISI interacted with each other, $F(7, 77) = 2.81, p < .05$. Finally, there was a significant three-way interaction between factors, Motion Bias, Position of the Odd Element, and ISI, $F(14, 154) = 4.83, p < .001$.

To investigate this three-way-interaction more closely in terms of the two critical bias conditions (element bias and group bias) we looked at a subset of the data, not including the no bias condition and collapsed over the factor Odd Color. The resulting three-factorial ANOVA with the factors Position of the Odd Element (left position, center position), Motion Bias (element bias, group bias), and ISI (0, 20, 40, 80, 120, 160, 200, or 300 ms) revealed main effects for all three factors, Position of the Odd Element, $F(1, 11) = 20.81, p < .001$, Motion Bias, $F(1, 11) = 74.33, p < .001$ and ISI, $F(7, 77) = 18.29, p < .001$. Furthermore, the factor ISI interacted with the factors Position of the Odd Element, $F(7, 77) = 3.45, p < .05$, and Motion Bias, $F(7, 77) = 3.65, p < .05$. The interaction between Motion Bias and Position of the Odd Element was not significant, $F(1, 11) = 0.008, ns.$, but the three-way-interaction between Position of the Odd Element, Motion Bias and ISI was significant, $F(7, 77) = 6.48, p = .001$. This pattern of results confirms what can be observed from the graph, suggesting that the dependence on ISI of the two motion bias conditions is different: The influence of the ISI in the group bias condition was stronger at shorter ISI than at longer ISI. The opposite was true for the element bias condition, for which the influence of ISI was stronger at longer ISI. Moreover, this effect was modulated by the position of the odd element, as the group motion ratings in the group bias condition were more dependent on ISI for the left position condition than for the center position condition. The inverse pattern, however, was observed for the element bias condition, as the group motion ratings increase more steeply for the center position condition than for the left position condition. Fisher LSD post hoc comparisons also confirmed this pattern of results, showing that for the element bias

condition of the left position condition only the last three comparisons were significantly different from the first ISI condition, whereas in the center condition all comparisons but the first were significantly different from the first ISI condition. For the group bias condition this pattern was reversed, as in the left position condition all ISIs were significantly different from the first ISI condition and the third ISI condition was significantly different from the second ISI condition. In the center position condition, however, none of the ISI conditions differed significantly from each other.

Figure 6 shows mean percent of group motion responses as a function of motion bias and interstimulus interval for Experiment 1B, collapsed over the factor odd color. Mean group responses were submitted to a three-factorial ANOVA with the factors Odd Color (green, blue), Motion Bias (no bias, element bias, group bias) and ISI (0, 20, 40, 80, 120, 160, 200, or 300 ms). As in Experiment 1A we found significant main effects for the factors Odd Color, $F(1, 11) = 7.28$, $p < .05$, Motion Bias, $F(2, 22) = 75.12$, $p < .001$ and ISI, $F(7, 77) = 24.03$, $p < .001$. Scheffé post hoc tests showed that all three motion bias conditions differed significantly from each other. Even though there was a main effect for odd color, the difference between the two color conditions was very small (56.69% vs. 58.78% for blue and green respectively) and the factor odd color did not interact with any other factor. The only significant interaction was found between the factor Motion Bias and ISI, $F(14, 154) = 23.94$, $p < .001$. Fisher LSD post hoc comparisons showed that this interaction is not only attributable to the no bias condition. Instead, it is caused by a differential influence of the ISI on the two bias conditions: In the group bias condition, none of the ISI conditions differed significantly from each other, whereas in the element bias condition the first four ISI conditions differed significantly from each other. This confirms the observation that in contrast to the element bias condition the group bias condition seems to be independent of the ISI.²

In summary, we found strong effects of luminance cues, contrast polarity as well as color and luminance, on correspondence resolution in Ternus displays, confirming similar previous findings (Dawson et al., 1994; Petersik & Rice, 2008).

Experiment 2

Can Nonluminance Features Influence Correspondence in Ternus Displays?

Luminance is an especially important cue for low-level theories of apparent motion. It is possible they, but not other types of feature cues, play a role in correspondence. To test this, the feature cues in the next two experiments were defined only on the basis of nonluminance differences, specifically orientation (Experiment 2A) and hue (Experiment 2B).

For Experiment 2A, the disks were Gabor patches that were tilted 45° either to the left or to the right. In Experiment 2B, the disks were two iso-luminant colors, turquoise and salmon.

²An additional ANOVA without the no bias condition showed an interaction between the factors ISI and motion bias, $F(7, 77) = 6.17$, $p < .01$, which also suggests that the interaction between the factor ISI and motion bias is not only attributable to the no bias condition. Furthermore, this analysis showed no main effect of the factor odd color, $F(1, 11) = 0.88$, ns, suggesting that the difference we found was entirely attributable to the no bias condition.

Otherwise the logic and design were the same as in Experiment 1B (in which only a single configuration was used).

Results and Discussion

The results confirmed that nonluminance cues, like luminance cues, can influence correspondence in Ternus displays. Figure 7 shows mean group responses as a function of motion bias and interstimulus interval for Experiments 2A and 2B, collapsed over the two types of orientation (45°-tilt to the left vs. 45°-tilt to the right) and two types of color conditions (turquoise-salmon-turquoise vs. salmon-turquoise-salmon), respectively.

For Experiment 2A a three-factorial ANOVA with the factor Odd Orientation (right tilt, left tilt), Motion Bias (no bias, element bias, group bias), and ISI (0, 20, 40, 80, 120, 160, 200, or 300 ms) was conducted. We observed significant main effects for the factor Motion Bias $F(2, 22) = 25.60, p < .001$ and ISI, $F(7, 77) = 26.59, p < .001$, but not for the factor Odd Orientation, $F(1, 11) = 1.86, ns$. Scheffé post hoc tests showed that the element bias condition was not significantly different from the no bias condition, but both conditions differed significantly from the group motion bias condition as the percent of group motion ratings were higher in the group bias condition (87.52%) than in the element bias (50.01%) and no bias condition (59.44%). The three-factorial ANOVA revealed also a significant interaction between the factor Odd Orientation and ISI, $F(7, 77) = 3.00, p < .05$ as well as between the factor Motion Bias and ISI, $F(14, 154) = 11.43, p < .001$. As in Experiments 1A (center position condition) and 1B the amount of group motion responses increased with the ISI more in the element bias condition than in the group bias condition, suggesting that the group bias condition is less dependent of the ISI than the element bias condition is. Fisher post hoc comparisons confirmed that for the group motion condition none of the ISIs differed significantly from each other, whereas in the element motion condition only the last four ISI conditions did not differ significantly from each other.

For Experiment 2B a three-factorial ANOVA with the within factors Odd Color (turquoise, salmon), Motion Bias (no bias, element bias, group bias) and ISI (0, 20, 40, 80, 120, 160, 200, or 300 ms) revealed a significant main effect of the factors Motion Bias, $F(2, 22) = 20.85, p < .001$, and ISI, $F(7, 77) = 53.68, p < .001$. The factor Odd Color, however, was not significant, $F(1, 11) = 2.83, ns$. Scheffé post hoc tests revealed that all bias conditions differed significantly from each other. Furthermore, there was a significant interaction between the factor Motion Bias and ISI, $F(14, 154) = 10.45, p < .001$, but no other significant interactions. Mean group responses increased with increasing ISI in the element bias and the no bias conditions, whereas they were mostly independent of ISI in the group bias condition, as the Fisher-LSD post hoc comparisons showed: only the first ISI differed significantly from all other ISIs in the group bias condition, whereas in the element bias condition the first three ISIs' differed significantly from each other.

In summary, correspondence in the Ternus display can be established not only on the basis of luminance as shown in Experiment 1, but also on the basis of non-luminance-defined features, such as orientation and hue (see Green, 1989 for a similar finding with another ambiguous motion display).³

Experiment 3: Is Correspondence Influenced by the Degree of Bias?

In the previous experiments, the element and group bias conditions yielded different patterns with regard to the extent to which they were dependent on ISI, the only spatiotemporal factor in these experiments. In particular in most group bias conditions, feature information overrode all influence of ISI, whereas feature information was less effective in the element bias conditions. Although, it is possible that for some reason group motion is more easily influenced by feature cues than element motion is, this difference also might derive from the fact that the feature cues in the element bias conditions were more ambiguous than they were in the group bias conditions. Specifically, the feature cue of the last disk in the element bias conditions was consistent with both element motion and group motion, whereas it was consistent only with group motion in the group bias condition (see Figure 3). In Experiment 3, we manipulated the degree to which the feature information, contrast polarity in this case, of the individual disks biased element and group motion. To do so, we manipulated the number of group-and element-bias compatible elements (see Figure 8). The two extreme conditions were the same as in Experiment 1A's center condition, 1B, 2A and 2B. In the other conditions we manipulated the individual Ternus disks such that they were more or less compatible with element and group motion. If correspondence processes are sensitive to these systematic changes in the number of compatible feature connections, then the influence of ISI should decrease with increasing feature compatibility.

Results and Discussion

The results confirmed that the strength of feature compatibility determines the relative effects of feature-differences versus ISI on the perception of Ternus motion. Figure 8 shows mean percent of group motion responses as a function of ISI and Degree of Bias collapsed over Odd Color. A three-factorial ANOVA with the factors Odd Color (white, black), Degree of bias (three-element-bias, two-element-bias, ambiguous, two-group-bias, three-group-bias) and ISI (0, 20, 40, 80, 120, 160, 200, or 300 ms) was conducted. The analysis revealed significant main effects for the factors Degree of Bias, $F(4, 44) = 24.51$, $p < .001$, as well as ISI, $F(7, 77) = 13.38$, $p < .001$, but not for the factor Odd Color, $F(1, 11) = 0.46$, ns. Group motion ratings for the degree of bias increased the more compatible the bias was with group motion (22.47, 34.53, 41.18, 57.58 and 89.58%). A Scheffé post hoc test for the factor Degree of Bias revealed that the 5th bias condition was significantly different from all others and the 4th bias condition was significantly different from the 5th and the 1st. Furthermore, the three-factorial ANOVA revealed a significant interaction between the factor Degree of Bias and ISI, $F(28, 308) = 4.55$, $p < .001$. No other interactions were significant. LSD post hoc tests comparing the different ISI conditions and degree of bias conditions statistically revealed different patterns for each of the different degree of bias conditions: for the three-group-bias condition none of the ISI conditions differed significantly from each other. For the two-group-bias condition only the longest ISI condition differed significantly from the second and the 6th ISI condition, all other comparisons were not significant. For the ambiguous condition even more comparisons were significant: the first ISI condition was

³In addition Green (1989) found that the influence of the color bias was larger when the background was iso-luminant with the discs. We found exactly the same with the Ternus display (experiment not reported here).

significantly different from all other ISIs, the second ISI conditions from all but its lower neighbor, the third ISI condition from all but its three lower neighbors. All other comparisons were not significant. For the two-element-bias condition all comparisons were significant with the exception of the nearest neighbors respectively. Finally, for the three-element-bias condition the first three ISI conditions, as well as the last five ISI conditions, were not significantly different from each other.

These findings suggest that the visual system takes into account each of the elements and establishes correspondence based on the best match. Overall, the more/fewer elements there were that were compatible with a group bias, the more/fewer group motion responses were given. Furthermore, the more compatible the feature information was with either a group or an element bias, the less dependent on ISI the percent of group motion responses became and the more dependent it was on feature cues. At first glance, the pure element bias condition seems to be an exception to this observation: for short ISI conditions, group motion responses are still dependent on ISI, even though in this condition all connections between disks are element bias compatible. However, the last two disks in both frames of this condition are compatible with a group bias, even though they are also compatible with an element bias. One would expect that a Ternus display using three different colors for each element and thus not allowing for a possible group bias connection of the last two elements would show even less dependence of ISI than what we find here. Indeed, in a comparable condition Petersik and Rice (2009, Experiment 1) found evidence consistent with this prediction.

In summary, the findings of this experiment suggest that the visual system can weight spatiotemporal and feature information flexibly: The more ambiguous the feature information is the more the visual system seems to rely on spatiotemporal information, ignoring feature information (and allowing for switches in color of some of the disks if necessary); the more reliable the feature information is, the less ISI plays a role.

Experiment 4: Is Correspondence Influenced by Feature Similarity?

In the previous experiments we showed that to solve the correspondence problem the visual system takes into account feature information, being sensitive to small differences in the organization of these feature cues such that the features of every single element contribute to the solution of the correspondence problem. How can these results be reconciled with findings showing little or no influence of feature information (e.g., Burt & Sperling, 1981; Kolers & Pomerantz, 1971; Navon, 1976; Nishida & Takeuchi, 1990; Shechter, Hochstein, & Hillman, 1988; Ullman, 1979; Werkhoven, Sperling, & Chubb, 1993, 1994)? One possibility is that correspondence is determined on the basis of similarity, rather than identity. Even for spatiotemporal factors, there is a range of spatial and temporal proximities that are sufficient to support correspondence (e.g., Attneave & Block, 1973; Neuhaus, 1930). If this holds for features as well, then correspondence may be determined by associating the two stimuli that are most similar to each other.

We addressed this question by asking whether or not feature cues need to be identical to influence the solution of the correspondence process or whether correspondence can be

established between the most similar elements in the display as well. Using the same logic as the previous experiments, we introduced either an element or a group bias in the Ternus display. In this case, however, none of the elements were identical across frames. Rather, they were just more or less similar. In Experiment 4A, a black element in the first frame was paired with a dark gray element in the second frame, and a white element in the first frame was paired with a light gray element in the second frame. In Experiment 4B we increased the difference between the elements from one frame to the next by pairing black elements with blue elements and white elements with green elements (the similarity here was determined, in part, by luminance). Finally, in Experiment 4C, we eliminated the luminance difference between the different colors in Experiment 4B by using three different iso-luminant colors, that weren't more or less similar to each other. If correspondence is established between the most similar elements, rather than just through identity, then there should be a difference between the group and the element bias condition. If instead correspondence is determined by identity alone, then no effect of the different feature-bias manipulations should occur. In addition, the less strong the similarity between the different elements is, the less strong this cue to correspondence should be weighted by the visual system leading to less difference between the different conditions and more dependence on ISI.

Results and Discussion

The results indicate that feature similarity is sufficient to influence correspondence in Ternus displays. Figure 9 shows mean group responses as a function of motion bias and interstimulus interval for Experiments 4A, 4B, and 4C, collapsed over different color conditions. A three-factorial ANOVA with the factors Odd Color (Exp 4A: white/light gray and black/dark gray; Exp 4B: white/green and black/blue), Motion Bias (no bias, element bias, group bias), and ISI (0, 20, 40, 80, 120, 160, 200, or 300 ms) was conducted for Experiment 4A and 4B. The analysis for Experiment 4A revealed significant main effects of the factor Motion Bias, $F(2, 22) = 30.74$, $p < .001$ and ISI, $F(7, 77) = 23.34$, $p < .001$. Furthermore, there was a significant interaction between these two factors, $F(14, 154) = 16.12$, $p < .001$. But there was no main effect of Odd Color and no significant interactions with the factor Odd Color. Scheffé post hoc tests for the factor Motion Bias revealed that all three bias conditions were significantly different from each other. Analyzing each motion bias condition separately for the influence of the ISI, Fisher-LSD post hoc comparisons between the different ISI revealed for the group bias condition none of the different ISI levels were significantly different from each other with one exception, namely that the fourth ISI was significantly different from the last two ISIs. For the element condition, on the other hand, the first two ISIs differed significantly from all other ISI levels and the third ISI as well as the fifth ISI differed significantly from the last ISI, but none of the other comparisons were significant.

The analysis of Experiment 4B revealed significant main effects of the factor Motion Bias, $F(2, 22) = 7.69$, $p < .01$, the factor Odd Color, $F(1, 11) = 18.39$, $p = .001$, and the factor ISI, $F(7, 77) = 41.93$, $p < .001$. The only significant interaction was observed between the factor Motion Bias and ISI, $F(14, 154) = 6.62$, $p < .001$. Scheffé post hoc tests for the factor Motion Bias revealed that the element motion condition differed significantly from the group

motion condition. A post hoc comparison for the factors Motion Bias and ISI revealed that in all bias conditions almost all comparisons were significant, suggesting that ISI played a role for all motion bias conditions, as can be also seen in the right graph of Figure 9.

For Experiment 4C a two-factorial ANOVA with the factors Motion Bias (no bias, element bias olive-salmon, group bias olive-salmon, element bias olive-pink, group bias olive-pink) and ISI (0, 20, 40, 80, 120, 160, 200, or 300 ms) revealed that only the factor ISI was significant, $F(7, 77) = 108.76$, $p < .001$, neither the main effect of Motion Bias, $F(4, 44) = 1.55$, ns, nor the interaction between both factors was significant, $F(28, 308) = 0.81$, ns. Mean percent of group responses increased with increasing ISI, but no effect of the motion bias on correspondence was found.

The results of these three experiments indicate that feature similarity, not just feature identity, can determine correspondence in Ternus displays. In addition, the more dissimilar the items are, the more influence ISI (the spatiotemporal variable in these displays) has on correspondence. This suggests again that the visual system weights the different cues for correspondence flexibly and takes those that are less ambiguous more into account.

Finally, these findings have important implications with regard to the apparent contradiction in the literature between studies that on the one hand show an influence of features on correspondence and studies on the other hand that do not. Specifically, they suggest two important possibilities. First, with regard to the influence of feature cues on correspondence, if there is no identity match, then the most similar item will contribute to the resolution of correspondence. Notice that this means that if there is only a single item with which correspondence could be established, then that item will necessarily be the most similar, even if it is quite different. This would provide an explanation for why little or no influence of features is found in simple apparent motion studies in which only two elements are presented, (e.g., Kolers & von Grünau, 1976; Kolers & Pomerantz, 1971). Second, it seems likely that the visual system can flexibly weight what information determines correspondence, based on its level of ambiguity. Thus if the feature difference between two elements is large, then spatiotemporal information may be weighted more strongly, whereas the reverse may be true if the feature difference is small or zero and the spatiotemporal information is ambiguous.

General Discussion

This study investigated the role of feature information in resolving correspondence within dynamic displays. This is an important question because objects in the environment change position and appearance frequently over time and the visual system has to be able to maintain correspondence in spite of this. We used the Ternus display because the two different percepts of this ambiguous motion display—element motion and group motion—reflect two very different solutions to object correspondence within the display. This study provides clear evidence that features (contrast polarity, color/luminance, orientation, and hue) influence correspondence in Ternus displays (Experiments 1–2), and that the degree of influence is determined systematically by the degree of element-level compatibility across displays (Experiment 3). Importantly, and contrary to the idea that spatiotemporal variables

dominate correspondence that is prevalent both in the apparent motion and object representation literatures, feature information can override the influence of spatiotemporal information (ISI), thus highlighting the flexibility of the visual system to rely on different types of information, depending on the relative ambiguity of a given source of information. Finally, the results of Experiment 4 indicate that it is the similarity of features, rather than identity, that influences correspondence. In this way feature identity is simply extreme similarity. This last finding provides an explanation for many of the apparent inconsistencies in the literature with some studies finding effects of features on correspondence and others not. Furthermore, the degree of similarity is an important factor that can predict how large the feature effect is compared with the influence of ISI. The weaker similarity becomes, the less it is taken as a reliable cue for correspondence.

We suggest that the ultimate solution to the correspondence problem is given by a flexible weighting of all of the variables available, without any special status given to spatiotemporal variables. This view is consistent with similar proposals that have been made for object updating in visual working memory (Hollingworth, Richard, Luck, 2002; Hollingworth & Rasmussen, 2010; Richard, Luck, Hollingworth, 2008) selective attention (Tas, Dodd, & Hollingworth, 2012), and multisensory integration (Ernst & Banks, 2002). Under this view of flexible weighting, drawing a distinction between spatiotemporal variables and features, as there is a tendency to do in the object perception literature (e.g., Flombaum et al., 2009; Kahneman et al., 1991; Mitroff & Alvarez, 2007), is arbitrary and potentially misleading.

As noted, the finding that feature similarity is sufficient to drive correspondence in Ternus displays provides a possible explanation for the discrepancy in the apparent motion literature where some studies report little or no effect of feature information on the perception of the quality of motion in traditional apparent motion displays in which only one stimulus appears in a given frame (e.g., Kolers & Pomerantz, 1971). If there is only one stimulus with which correspondence can be established, that stimulus will be the most similar (see also Watson, 1986). As Experiment 4 showed, there is however an upper bound of dissimilarity beyond which correspondence will not be tolerated. If spatial and temporal proximity are considered in terms of similarity, then the large spatial and long temporal separations for which good apparent motion is no longer observed (e.g., Attneave & Block, 1973; Neuhaus, 1930) indicate the upper bounds of spatiotemporal “similarity.” It follows that the upper bound of featural similarity may not have been reached in those studies that find tolerance of correspondence between stimuli with different features.

The relative weighting of factors under the flexible-weighting view also provides an explanation for why feature information seems to strongly bias ambiguous motion in some displays, notably the Ternus display as shown here, but not, or much less, in others, such as the motion quartet or split motion displays. Specifically, the complexity of the apparent motion displays in terms of number and quality of alternative solutions to the correspondence problem will determine what factors are available for relative weighting. In motion-quartet displays, for example, in which one can perceive either horizontal motion or vertical motion (e.g., von Schiller, 1932; Ullman, 1979), biasing the displays so that elements match in form, color, or other features across the two horizontal pairs or the two vertical pairs often does not strongly bias which type of motion is perceived (e.g., Navon,

1976; Sterzer & Kleinschmidt, 2005). One possibly important difference between these displays and the Ternus display is that in the Ternus display there are three elements in each frame, instead of two, and therefore correspondence could, in principle, be established between any given element in the first frame and any given element in the second frame, possibly leading to contradicting signals.⁴ The complexity of the possible connections might prompt the visual system to use all available information, including feature information to solve the correspondence problem. In other words, it is again a question of taking into account all of the potential factors, weighting them according to some maximum likelihood principle, and resolving correspondence based on that process. Direct comparison of these different ambiguous apparent-motion displays would provide further insight into these ideas. The current study cannot speak directly to them.

A separate issue that should be considered regarding not only the current study but also other studies concerned with the question of how features do or do not influence the correspondence process is that the influence of feature information may be indirect. It is possible that the odd items in each Ternus frame attract attention and that correspondence is solved through the binding of the attended items. Experiment 4C, however, showed that there are feature conditions in which no bias for correspondence can be found, suggesting that the feature bias effects are not attributable to such a general attention effect but that the specific nature of the features is important to exert an effect on correspondence. This doesn't mean that attention cannot play a role. In particular, correspondence may be mediated by an attention-based motion system (Cavanagh, 1992) in which attentional pointers that take feature information into account provide information about displacements in space.

Finally, what implications do the current findings have for our understanding of apparent motion and the mechanisms behind the perception of motion in Ternus displays, in particular? An early proposal was that the two alternative percepts in the Ternus display—element and group motion—reflect two different motion processes, a short-range process responsible for element motion and a long-range process for group motion (e.g., Braddick & Allard, 1978; Pantle & Picciano, 1976; Petersik & Pantle, 1979). Although this two-process distinction has been challenged (e.g., Breitmeyer & Ritter, 1986a; Odic & Pratt, 2008, but see Petersik, 2010; see Dawson, 1991 for a review), most theories of the Ternus display have focused on low-level mechanisms (e.g., Braddick, 1980; Breitmeyer & Ritter, 1986a, 1986b; Pooremaeili, Cicchini, Morrone, & Burr, 2012). Breitmeyer and Ritter (1986a), for example, suggested that element motion occurs because of visible persistence of the central elements, and that the consequential lack of transients signals the system that there is no motion for these elements (but see Alais & Lorenceau, 2002; Kramer & Rudd, 1999).

Various studies showing an influence of ISI and luminance and stimulus duration and other factors affecting visual persistence supported this low-level influence (e.g., Petersik & Pantle, 1979). More recent studies, however, have challenged this view by showing that even when ISI and contrast are held constant, the Ternus display can be biased to yield percepts of either element or group motion, depending on other factors, such as perceptual grouping

⁴The same holds for split motion displays, in which generally no feature influence is found (e.g., Nishida & Takeuchi, 1990; Nishida, Ohtani, & Ejima, 1992; Werkhoven, Sperling & Chubb, 1993; 1994; but see Ramachandran, Ginsburg, & Anstis, 1983).

principles and stimulus context effects (Alais & Lorenceau, 2002; Boi et al., 2009; Hein, & Moore, 2010; Kramer & Yantis, 1997; He & Ooi, 1999; Ma-Wyatt et al., 2005; Petersik & Rice, 2008; Wallace, Scott-Samuel, 2007). In line with these newer studies, the current experiments yielded different amounts of group and element motion responses despite constant strength of the transients in the display. In particular, in the element bias conditions we found a decrease in group motion responses compared with the no bias condition, despite of no change in features (or the temporal gap between them) at the location of the central elements (this is especially striking if one compares the two conditions with the strongest element bias in Experiment 3 that show different amounts in group motion responses even though both center elements are identical). This does not mean, however, that low-level factors do not play a role at all in our displays. In particular, low-level factors could be more important in unambiguous and simpler displays in terms of the number of potential correspondence solutions, whereas higher-level factors could play a more dominant role in more ambiguous and more complex displays.

In summary, we conclude that to solve the correspondence problem, the visual system uses whatever information is available to disambiguate ambiguous input, and that the impact of relative weightings is especially powerful when the solution to the correspondence problem is more complex. There is little reason to treat spatiotemporal and feature factors as qualitatively different. Rather, how much the visual system relies on each of the factors depends on how reliable the information is. If feature information is unambiguous, then it will be able to override any effect of spatiotemporal information. At the same time the system is flexible enough to tolerate changes in features if the spatiotemporal relationship strongly suggests that the object is the same and accommodates perception in line with it.

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Figure 1.

Illustration of two factors that can, in principle, be used by the visual system to solve the correspondence problem. A (left), Correspondence on the basis of spatiotemporal proximity leads to B, not C, being perceived as the same object as A. B (right), Correspondence on the basis of feature identity leads to B, not C, being perceived as the same object as A.

Figure 2.

Two solutions to the correspondence problem in the Ternus Display, leading to two alternative percepts. With element motion, the second and third discs (B and C) correspond to the first and the second discs (B' and C') in the second frame, whereas the first disc (A) corresponds to the last disc in the second frame (A'). With group motion the first, second, and third discs (A, B, and C) in the first frame correspond to the first, second, and third discs (A', B', C') in the second frame.

Figure 3.

Overview of the different stimulus conditions used in the Ternus displays of all experiments (with the exception of Experiment 3). In the no bias condition (row 1) all discs are always identical. In the bias conditions features of the discs were chosen so that they either corresponded to the organization of the discs in terms of element motion (element bias condition, row 2) or in terms of group motion (group bias condition, row 3). In Experiments 1 and 2 the surface features from one frame to the other are identical, defined either by luminance (contrast polarity and color) or not luminance-defined feature values (orientation and hue). In Experiment 4 none of the discs' features in one frame are identical to the surface features in the other frame. In Experiment 4A and 4B they are similar in terms of luminance, in Experiment 4c there is no similarity in terms of luminance or hue.

Figure 4.

Illustration of the basic trial sequence (no bias condition). Each trial started with the presentation of a central fixation cross and a set of three discs for 200 ms. After a variable inter-stimulus interval between 0 and 300 ms, the set of discs is shifted one position to the right and presented for another 200 ms, followed by the same inter-stimulus interval. These two Ternus disc displays continue to alternate until a response key is pressed. Participants' task is to decide if they perceived element or group motion.

Figure 5.
Illustrations of different conditions in Experiment 1A (contrast polarity).

Figure 6.

Mean percent of group responses as a function of Inter-stimulus Interval and Motion Bias in Experiment 1A and 1B, in which the feature manipulation was based on contrast polarity as well as color and luminance. A, The no bias condition is the same in both graphs. Error bars represent the standard error of the mean in each condition.

Figure 7.

Mean percent of group responses as a function of Inter-stimulus Interval and Motion Bias in Experiment 2A (left), in which the feature manipulation was based on the orientation of Gabors, and Experiment 2B (right), in which the feature manipulation was based on hue (iso-luminant color). Error bars represent the standard error of the mean in each condition.

Figure 8.

Mean percent of group responses as a function of Inter-stimulus Interval and Motion Bias in Experiment 3, in which the number of discs that were compatible with element and group bias were systematically manipulated. Solid arrows indicate element bias connections, and dashed arrows indicate group bias connections. The error bars represent the standard error of the mean in each condition.

Figure 9.

Mean percent of group responses as a function of Inter-stimulus Interval and Motion Bias in Experiment 4A (left graph), in which the feature manipulation was based on similarity in luminance, and Experiment 4B (center graph), in which the feature manipulation was based on similarity of luminance and colors, and Experiment 4C (right graph), in which there was no difference in similarity between different elements. Error bars represent the standard error of the mean in each condition.