Visual Working Memory Content Influences Correspondence Processes

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Representing objects as continuous across time requires the establishment of correspondence, whereby current stimuli are represented as deriving from the same object as earlier stimuli. Spatiotemporal continuity and surface-feature similarity play important roles in these correspondence processes. Because objects are often represented across extended periods of time, visual working memory (VWM) content should also play a role in object correspondence. We tested this prediction using Ternus motion. Displays consisted of three-disk arrays that shifted horizontally by one position between frames. Depending on how correspondence is resolved, Ternus displays are perceived as *group motion,* where all three disks appear to move together, or *element motion,* where one disk appears to jump across the others. Reports of which motion is perceived provide an index of how correspondence was resolved. Ternus displays were adapted such that the color of some disks biased element motion while the color of others biased group motion. Maintaining one or the other of the colors in VWM for later report systematically biased which type of motion was perceived (Experiments 1 and 2). When color was incidental to the VWM task, however, it did not (Experiment 3). These results confirm that VWM content contributes to object correspondence.

Public Significance Statement
When an object moves, it can disappear or change appearance due to spurious changes like lighting conditions, and yet we perceive it as a stable entity that exists continuously over time. This is an achievement that artificial vision systems struggle to master. The current study demonstrates that specific attributes that we hold in memory can systematically influence how the visual system determines which objects belong together across space and time, but only when the attributes are relevant to the current task. This research expands our understanding of how the human visual system represents objects as continuous over time, knowledge that could be used to improve artificial vision systems.

Keywords: perceptual organization, motion correspondence, visual working memory, apparent motion, Ternus display

A central function of the visual system is to establish and maintain representations of objects that are continuous over time. It does this despite movements of the objects and movements of images of the objects on the retina due to head, body, and eye movements of the viewer. Moreover, it does this despite changes

in the context in which objects appear (e.g., light to shadow), and changes in attributes of the objects (e.g., when a friend gets a new hair cut). The problem, which was referred to originally in the motion perception literature as the *correspondence problem* (Ullman, 1979), has been characterized by Dawson and colleagues as the problem of knowing "what went where?" (Dawson, 1991). The idea is that objects in the world exist over time and space, and they can project different images at different times, including no image at all when an object is out of view for brief periods of time, as when it moves behind other objects. For example, when your child is on a carousel and disappears out of sight on her way around the pole, you perceive her as moving behind the pole, not as disappearing momentarily and reappearing later. Objects, more generally, continue to exist over even longer periods of time than this example, as when friends do not see each other for weeks and yet are able to easily recognize each other when they meet again. Despite discontinuous visual input, we can and do represent objects as continuous entities, and we update their representations on the basis of new information when it becomes available. The correspondence problem is the question of how the visual system

comes to associate newly available visual information with the "correct" existing object representation, rather than with another object representation, or with no object representation at all, thereby requiring the establishment of a new object representation.

The "problem" part of the correspondence problem is the question of on what basis correspondence is established. Two broad hypotheses have dominated the literature. According to the *spatiotemporal priority hypothesis*, correspondence is based on spatiotemporal information (e.g., Flombaum et al., 2012; Pylyshyn, 2001; Scholl, 2001). The idea is that if the temporal and spatial relations between two stimuli are consistent with the mechanics of how a physical object could move (or remain stationary) over time, then correspondence will be established, and a single object will be perceived, with the two stimuli reflecting different states of that object. The strongest version of this hypothesis asserts that featural differences other than spatiotemporal factors, such as color and shape, are irrelevant. Under this view, if other features are different when correspondence is established based on spatiotemporal coherence, then the difference will be accommodated, such as when an object is perceived as morphing in shape when apparent motion is perceived between two differently shaped stimuli that are presented in quick succession at nearby locations (Burt & Sperling, 1981; Navon, 1976; Navon, 1983; Kolers & Pomerantz, 1971; Kolers & von Grünau, 1976). The alternative hypothesis to spatiotemporal priority asserts that although spatiotemporal coherence plays a significant role in establishing correspondence, so do the features of objects, such as color and shape. Under this view, correspondence is resolved on the basis of whatever balance of information provides the least ambiguous solution to the corre-

spondence problem (Hein & Cavanagh, 2012; Hein & Moore, 2012; Hein & Moore, 2014; Hollingworth & Franconeri, 2009; Hollingworth & Matsukura, 2019; Richard et al., 2008).

On the face of it, it seems that correspondence must be based on feature information, including shape and surface features, for longer-term correspondence as with the parting-friends example (e.g., Riesenhuber & Poggio, 1999). But at this point there is also substantial evidence that surface features are used to resolve correspondence across short stimulus intervals as well, and can even dominate spatiotemporal factors. Much of that evidence comes from experiments using some form of ambiguous apparent motion to test what factors tip the balance in favor of one percept or another (e.g., Burt & Sperling, 1981; Dawson et al., 1994; Green, 1986; Hein & Moore, 2012; Shechter et al., 1988; Ullman, 1979; von Schiller, 1933). Ternus motion is an example (Pikler, 1917; Ternus, 1926). In a Ternus display, an array of (usually) three adjacent elements is presented in alternation with the same set of elements shifted by one position (Figure 1A). In this ambiguous motion display the elements can be perceived as moving all together (*group motion*) or as one element jumping across the other two, which remain stationary (*element motion*). Notice that the two different perceptions of Ternus displays—group motion versus element motion—imply mutually exclusive alternative solutions to the correspondence problem. Therefore, which type of motion is reported can be used as a measure of how correspondence was resolved under a given set of conditions. A strong determinant of whether group or element motion is perceived, and by inference therefore how correspondence is resolved, is the time between the two displays, or the *interstimulus interval* (ISI). Spe-

Figure 1
Different Types of Color-Based Feature Biases in the Ternus Display
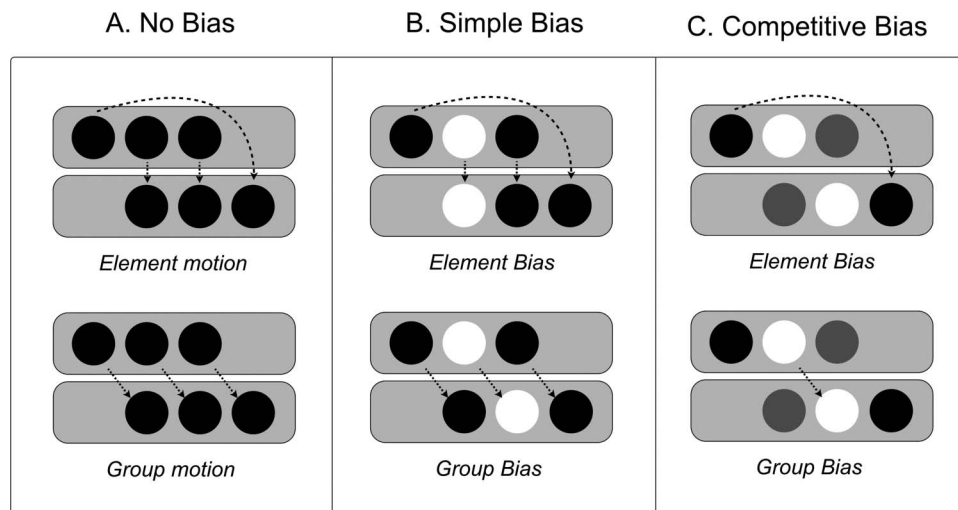
Note. A. Standard no-bias display in which all items are the same color. In this display correspondence is influenced by the interstimulus interval (ISI): For short ISIs element motion is seen (upper), for long ISIs group motion is seen (lower). B. In a simple feature-bias display, the Ternus elements have different colors/luminances, being consistent with either element motion (upper) or group motion (lower), leading to the corresponding motion percepts being seen more frequently. C. In the competitive-bias display, one color of the Ternus elements is consistent with element motion and inconsistent with group motion (here black), while another color is consistent with group motion and inconsistent with element motion (here white). Percepts in this display tend to be independent of ISI and maximally ambiguous.

cifically, at long ISIs, group motion tends to be perceived, whereas at short ISIs, element motion tends to be perceived (e.g., Breitmeyer & Ritter, 1986; Petersik & Pantle, 1979). Because ISI is a spatiotemporal variable, the fact that the perception of Ternus motion depends on it is consistent with the spatiotemporal priority hypothesis. It has also been shown, however, that whether group or element motion is perceived can be strongly biased by the surface features of individual elements (e.g., Alais & Lorenceau, 2002; Casco, 1990; Dawson et al., 1994; Hein & Moore, 2012; Kramer & Rudd, 1999; Kramer & Yantis, 1997; Petersik & Rice, 2008; see Moore et al., 2020). Figure 1B illustrates an example in which color is used to bias either element (upper display) or group (lower display) motion. Feature biases of this sort strongly influence how Ternus displays are perceived, and can even completely dominate any influence of ISI (Hein & Moore, 2012; Petersik & Rice, 2008).

Given that surface features can influence correspondence as strongly as spatiotemporal coherence does, a further question is what level of surface feature representation is critical (He & Nakayama, 1994; Hein & Moore, 2014; Stepper, Moore, et al., 2020a)? Is it the similarity of features as they exist in the image itself, such as luminance, image size, and image shape, or is it the similarity of features as they are abstracted from the image to represent objects in the world, such as perceived reflectance (i.e., *lightness*), perceived size, and perceived shape, which are representations that discount differences in apparent illumination and depth? This question was addressed by adding regions of apparently different illumination conditions and occluding surfaces to Ternus displays, which provided separate assessments of the impact of perceived features and image-level features on object correspondence (Hein & Moore, 2014; see also Palmer et al., 1996; Rock & Brosgole, 1964; Rock et al., 1992 for this strategy applied to perceptual grouping in static displays). This and related work showed that correspondence is influenced not only by the luminance, image size, and image shape of elements across frames, but also by the perceived lightness, perceived size, and perceived shape of elements (He & Nakayama, 1994; Hein & Moore, 2014; Stepper, Moore, et al., 2020a).

The aim of the current work was to extend this line of questioning to ask whether Ternus motion can be biased on the basis of visual working memory (VWM) content, which is based on feature information that is not present in the image at the time that correspondence is established. The function of object correspondence is to support the representation of objects as entities in the world that exist over time, even when they are not visible for periods of time. For example, it has been proposed that object correspondence across the perceptual gap created by a saccade depends on VWM (Hollingworth et al., 2008), and manipulations of VWM have been shown to bias this correspondence operation (Hollingworth & Luck, 2009). It follows, therefore, that information in memory should be capable of contributing to the correspondence process in the perception of motion. To test this prediction, we added a working memory task to competitive-bias Ternus displays (Hein & Schütz, 2019; Stepper, Rolke, et al., 2020) and asked whether the content held in VWM would systematically bias which type of motion was perceived. The strategy is analogous to that used to test whether VWM content biases the control of visual attention (e.g., Olivers et al., 2006; Soto et al., 2005).

Figure 1C illustrates a competitive-bias Ternus display. The elements differ in color such that one color is consistent with element motion and inconsistent with group motion, while another color is consistent with group motion and inconsistent with element motion. Prior to these displays, observers were shown a patch of color to hold in VWM for later report. The memory color could match the group-bias color, the element-bias color, or neither (see Figure 2A). We found that reports of group or element motion were systematically biased by these color matches (Experiment 1). We ruled out the possibility that the biases were strategic (Experiment 2). In particular, participants might have attended to the Ternus element with the same color as the memory color to help their memory, which in turn could have influenced correspondence (Stepper, Rolke, et al., 2020). And finally, we found that when the memory task was to remember a shape, and therefore that color was only incidentally part of the to-be-remembered stimulus, color did not influence correspondence (Experiment 3).

Experiment 1: Simple Color Memory Task

At the beginning of each trial, subjects were shown a colored rectangle and asked to remember the color. Next, a Ternus display was presented with either competitive-bias displays (Figure 1C; half of the trials) or no-bias displays (Figure 1A; other half of the trials). Figure 2A illustrates the conditions. For competitive-bias displays, the memory color could match one of the three colors, the group-bias color (GB-Match), the element-bias color (EB-Match), or the third color (Third-Match), or it could match none of the colors in the Ternus display (No-Match). The hypothesis is that activating a given color as a trace in VWM will enhance the processing of elements of that color in the competitive Ternus display, thereby biasing the type of motion that this color is consistent with. We expected, therefore, to find more group motion reports in the condition in which the memory color matched the group-bias color compared to the element-bias color condition. As a control, we also used no-bias displays, in which the memory color either matched the elements in the Ternus displays (Match) or did not (No-Match). We did not expect memory color to influence correspondence in this case, as all the elements were identical and thus correspondence should be based on the ISI between Ternus frames.

Method

Participants

Twelve observers participated in Experiment 1 (mean age 20 years). They were members of the University of Tübingen community, and received either credit for a research-experience requirement or 7 Euro in compensation for their time. Participants were naïve as to the purpose of the experiment and all reported normal or corrected-to-normal visual acuity and color vision. Choice of sample sizes was based on power analyses that used estimates of adjusted partial eta squared (Mordkoff, 2019) from a previous study that tested the effect of attentional cueing on the perception of competitive Ternus displays (Stepper, Rolke, et al., 2020). Sample sizes of 5 and 11 were calculated from two separate experiments as being necessary to achieve .8 power, assuming an

Figure 2
Illustration of Memory Color Conditions Used in the Three Experiments
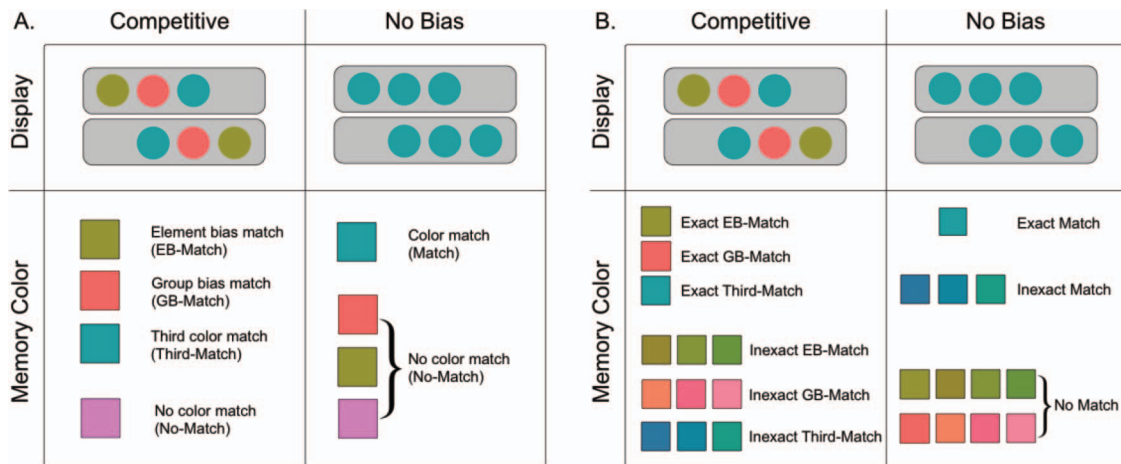
Note. A. Experiments 1 and 3: In the competitive-bias display condition, the memory color can either match the element bias compatible color (here olive-green), the group bias compatible color (here salmon), the third color used (here turquoise), or none of the elements' colors (here pink). In the no-bias display condition, the memory color can either match the color of the Ternus elements (here turquoise) or not. B. Experiment 2: The same competitive-bias and no-bias Ternus conditions were used as in Experiment 1 and 3. The color match could, however, either be an exact match or not, the memory color being randomly chosen from one of the other three colors within the same color category. In the no-match condition, the memory color was randomly chosen from one of the colors of the other two color categories. See the online article for the color version of this figure.

alpha of .05. To be conservative, we therefore planned a sample size of 12 for each of the experiments reported here.

Equipment

Stimuli were presented using a PC with Windows XP driving a 17-in. color monitor with a spatial resolution of 1024 × 768 and a refresh rate of 100 Hz. The experiment was controlled with MATLAB software (Version 7.4 release 2007a, Mathworks, MA) and the Psychophysics toolbox extensions (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997). Viewing distance was fixed at 65 cm. The experiments were conducted in a dimly lit individual testing room.

Stimuli

The memory color was a 1.50° square presented at the center of the monitor. It was one of four photometrically equiluminant colors: turquoise (RGB: 0, 140, 140; 22 cd/m²), olive-green (RGB: 132, 132, 0; 22 cd/m²), pink (RGB: 225, 10, 225; 22 cd/m²), and salmon (RGB: 142, 67, 67; 22 cd/m²). Ternus displays consisted of two frames of three circular elements (1.50° diameter), presented sequentially with a variable ISI between them. The elements in a given frame were separated center-to-center by 1.50° and shifted one position to the right across the two frames. These displays were presented such that the four element positions of the combined first and second frame were centered horizontally, 1.32° above a central fixation cross (0.26° × 0.26°). For no-bias displays, all of the elements were displayed in one of the four colors. For competitive-bias displays, the three Ternus elements were presented in different colors, as illustrated in Figure 1C. The middle elements in the first and second Ternus frames were the same color. The outer two elements in the two frames were the

same color as each other, but were a different color from the middle elements. And finally, the last element in the first frame and the first element in the second frame were also the same color as each other, and different from the other two pairs of elements. Which color was used for which element pair was selected randomly. This configuration established two competing color biases. Specifically, the color of the middle elements creates a match that is consistent with group motion, and inconsistent with element motion, whereas the color of the two outer elements creates a match that is consistent with element motion and inconsistent with group motion. The third color match is consistent with neither group nor element motion. Finally, following the Ternus display on each trial, two colored 1.50° squares were presented 2.80° to the left and right of fixation. One square (its left or right position randomly selected) was the same color as the square presented at the beginning of the trial (*target*), and the other square was a different color, randomly chosen among the three remaining colors (*foil*).

Task

At the end of the trial, participants first reported whether they perceived group or element motion using the "j" and "f" keys on the computer keyboard, respectively. Next, the memory probe display was presented, and participants indicated whether the left or the right rectangle was the same color as the rectangle presented in the beginning of the trial, using the "j" and "f" keys, respectively.

Procedure

Participants were tested individually in single 50-min sessions. They first read and signed an informed consent form in accordance

with the ethical guidelines of the declaration of Helsinki (World Medical Association, 2013). After written instructions on the computer screen, participants were shown two examples of a no-bias Ternus display in which observers usually perceive element motion (the shortest ISI between Ternus frames presented during the experiment: 0 ms ISI) and group motion (the longest ISI between Ternus frames presented during the experiment: 300ms). The Ternus display was first presented as cycling continuously to give the observer more time to see the motion. After that a one-cycle version was presented as in the experiment itself. After 16 practice trials of initial familiarization with the different displays, participants completed 8 blocks of 48 experimental trials each. A break was provided every 24 trials.

Trial events are illustrated in Figure 3. Each trial began with the fixation cross for 800 ms. Following a 500-ms blank interval, the memory color was presented for 300 ms, followed by a 1200-ms blank interval. The fixation cross and the first Ternus frame were then presented for 200 ms, followed by a variable ISI between 0 and 300 ms and the second Ternus frame for another 200 ms. The fixation cross remained on the screen until a key press was recorded. If a key other than the "j" or "f" was pressed, a written error message was presented for 1000 ms, otherwise a blank screen was presented for 500 ms. The fixation cross was then presented again for 800 ms, followed by the memory-probe display until a keypress was made. A tone with frequency of 1200 Hz for 200 ms and a written feedback for 1000 ms was provided if the foil was selected instead of the target, or if any key other than the two response keys was pressed. After a 1000-ms intertrial interval, the fixation cross for the next trial was presented.

Design

A 4 (Memory Color: EB-Match, GB-Match, Third-Match, No-Match) × 2 (Display: competitive-bias, no-bias) × 6 (ISI: 0, 20, 40, 80, 160, 300 ms) within-subjects design was used. All factors were completely counterbalanced and mixed randomly within each block for a total of 8 repetitions. For the no-bias condition, all three match conditions were the same as the single color used for all the elements in the Ternus display, and therefore the "EB-Match," "GB-Match," and "Third-Match" conditions were all the same for no-bias trials.

Data Analysis

We planned to replace participants who had a mean error rate in the memory task higher than 25%. No participant met this criterion in Experiment 1. The mean error rate across participants was 7.23%. Trials with key presses other than the response keys (0.28%) and extremely long RTs (>8000 ms, 0.04%) were eliminated.

For our analyses of variance (ANOVAs), Greenhouse-Geisser corrections were used to account for violations of the sphericity assumption when they occurred. Alpha was set to .05. Post hoc comparisons were Holms corrected. Effect sizes are reported in terms as adjusted partial eta-squared ($adj.\ \eta_p^2$), which is an estimate of partial eta-squared that adjusts for the known positive bias in

Figure 3
Trial Sequence of Experiment 1
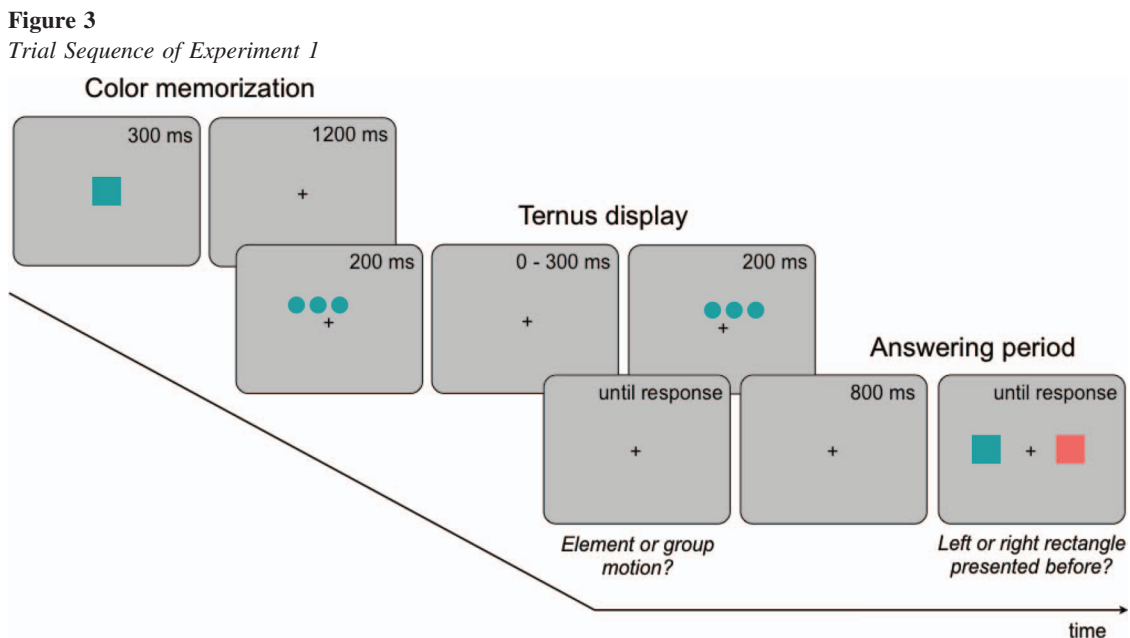
Note. In the beginning of the trial, a fixation cross was presented for 800 ms followed by a blank screen for 500 ms (not illustrated). Then participants had to memorize the color of the rectangle presented at the center of the screen (Color memorization). Next, the Ternus display was presented. In the end of the trial participants had to indicate which type of Ternus motion they saw (Answering period), followed by a blank interval for 500 ms or an error message if a nonresponse key was pressed (not illustrated). Finally, after another fixation interval of 800 ms, two differently colored rectangles were presented and participants had to indicate which rectangle had the same color as the memory probe of the beginning of the trial. If necessary, an error feedback was given (not illustrated). See the online article for the color version of this figure.

that measure (Mordkoff, 2019). All analyses were done using R (R Development Core Team, 2008).

Results and Discussion

Mean group-motion responses are shown for competitive-bias and no-bias displays separately in Figure 4. We first conducted an overall 2 (Display: competitive-bias, no-bias) × 4 (Memory Color: EB-Match, GB-Match, Third-Match, No-Match) × 6 (ISI: 0, 20, 40, 80, 160, 300 ms) repeated-measures ANOVA on individual mean group-motion responses. It revealed a main effect of Display, $F(1, 11) = 11.39$, $p = .006$, $adj. \eta_p^2 = .46$, as well as an interaction between Display and Memory Color, $F(3, 33) = 7.67$, $p = .001$, $adj. \eta_p^2 = .36$, but only a trend for the interaction between Display and ISI, $F(5, 55) = 2.47$, $p = .096$, $adj. \eta_p^2 = .11$, and no three-way interaction, $F(15, 165) = 0.92$, $p = .544$, $adj. \eta_p^2 = -.01$.

We next conducted separate analyses for the two display conditions. Individual mean group responses for the competitive-bias display (Figure 4, left) were submitted to a 4 (Memory Color: EB-Match, GB-Match, Third-Match, No-Match) × 6 (ISI: 0, 20, 40, 80, 160, 300 ms) repeated-measures ANOVA. There was no main effect of ISI, $F(5, 55) = 2.25$, $p = .150$, $adj. \eta_p^2 = .09$, but there was a main effect of Memory Color, $F(3, 33) = 12.41$, $p = .001$, $adj. \eta_p^2 = .49$, and there was no interaction between Memory Color and ISI, $F(15, 165) = 1.24$, $p = .246$, $adj. \eta_p^2 = .02$. Follow-up comparisons confirmed what is apparent in the figure. Group-motion reports were significantly higher in the GB-Match condition (57%) than in the EB-Match condition (42%), $t(11) = 3.58$, $p_{holm} = .016$, $adj. \eta_p^2 = .50$. In addition, they were higher in the No-Match condition (54%) than in the EB-Match condition

(42%), $t(11) = 3.74$, $p_{holm} = .016$. $adj. \eta_p^2 = .52$. Finally, group motion responses were higher in the GB-Match condition (57%) than in the Third-Match condition (42%), $t(11) = 3.72$, $p = .016$, $adj. \eta_p^2 = .52$, and in the No-Match condition (54%) compared to the Third-Match condition (42%), $t(11) = 4.68$, $p = .004$, $adj. \eta_p^2 = .64$. The remaining two comparisons between the GB-Match and the No-Match conditions, and between the Third-Match and the EB-Match conditions, were not significant, $-1.40 < = t < 0.38$, $p > = .377$, $adj. \eta_p^2 < .07$. In an additional analysis, we examined the effect of the ISI in more detail by analyzing each Memory Color condition separately. We found a significant effect of the ISI in the GB-Match condition, $F(5, 55) = 3.88$, $p = .032$, $adj. \eta_p^2 = .19$, but no effect of the ISI in any of the other three Memory Color conditions, EB-Match, $F(5, 55) = 0.47$, $p = .799$, $adj. \eta_p^2 = -.05$, Third Match $F(5, 55) = 2.28$, $p = .122$, $adj. \eta_p^2 = .10$, and No Match $F(5, 55) = 0.31$, $p = .776$, $adj. \eta_p^2 = -.06$.

Next, mean group-motion responses in the no-bias display condition (Figure 4, right) were submitted to a 2 (Memory Color: Match, No-Match) × 6 (Inter-Stimulus Interval: 0, 20, 40, 80, 160, 300 ms) repeated-measures ANOVA. For no-bias displays, there was a main effect of ISI, $F(5, 55) = 4.25$, $p = .032$, $adj. \eta_p^2 = .21$, confirming that group motion responses increased with increasing ISI from 62% at the 0-ms ISI to 92% at the 300 ms-ISI. The main effect of Memory Color, however, was not significant, $F(1, 11) = 0.37$, $p = .554$, $adj. \eta_p^2 = -.06$, and there was no interaction between ISI and Memory Color, $F(5, 55) = 0.34$, $p = .885$, $adj. \eta_p^2 = -.06$.

The results from Experiment 1 demonstrate that visual working memory content can bias correspondence, as revealed by the perception of Ternus motion: Those elements whose color

Figure 4
Results of Experiment 1: Mean Percent of Group Motion Responses as a Function of ISI and Memory Color
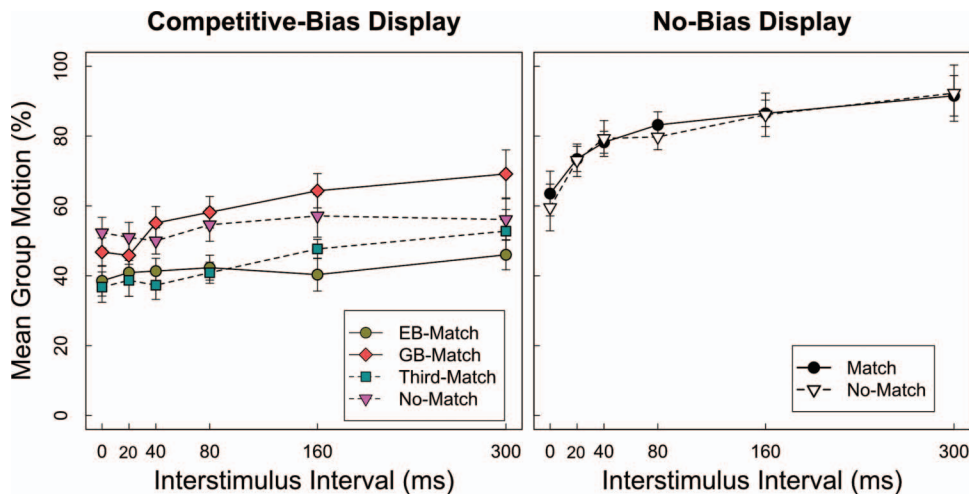
Note. The left graph shows the competitive-bias display condition for each of the four memory color conditions, element bias match (EB-Match), group bias match (GB-match), third color match (Third-Match), or no color match (No-Match). The right graph represents the no-bias display condition for each of the two memory color conditions, either matching the element's color (Match) or not (No-Match). Standard errors represent within-subject SEs after Cousineau-Morey (Cousineau, 2005; Morey, 2008). ISI = interstimulus interval. See the online article for the color version of this figure.

matched the color being held in visual working memory dominated the type of motion perceived. Specifically, when the memory color matched the group-bias color, more group motion was perceived, and when it matched the element-bias color, less group motion was perceived. The results from the no-bias display were also as expected. Without any competing feature information, correspondence, and the resulting perception of group versus element motion, was influenced only by ISI such that more group motion was perceived at longer ISIs (e.g., Petersik & Pantle, 1979; Pikler, 1917; Ternus, 1926). Moreover, we also found an influence of the type of display (competitive-bias vs. no-bias) on the strength of the ISI effect: When feature information was conflicting with regard to the correspondence of elements across frames of motion in the competitive-bias displays, ISI had a less strong effect on whether group or element motion was perceived compared to the no-bias display. In addition, the ISI had an effect when the memory color matched the group bias as compared to the element bias (or third color). The lack of an effect of ISI in the competitive-bias display without any additional bias (No-Match condition) has been shown before (Stepper, Rolke, et al., 2020), and is consistent with the assertion that feature information, which favors neither group nor element motion in the case of competitive-bias displays, can influence Ternus motion as strongly as ISI does. More mysterious is the finding that there was a small effect of the ISI when the memory color matched the group bias. We can only speculate as to what the reason for this difference is. One possibility is that a correct feature mapping in the element bias case could be maintained if in addition to the first element jumping over the other two, the two middle elements appeared to swap places, a solution that might have satisfied the visual system at any ISI. In contrast, in the case of the group bias such a perfect mapping is impossible, leaving some room for the effect of the ISI to determine the response as well. Future research should address this speculation by asking more specifically about the exact percept the participants perceive.

It is possible that the influence of VWM content in this experiment reflects a strategic use of colored elements in the Ternus displays to facilitate the memory task, rather than a more general interaction between memory content and correspondence processes. Specifically, it is possible that in order to refresh a memory trace, participants strategically attended to elements of the same color. Because attending to individual elements can influence how Ternus displays are perceived (Stepper, Rolke, et al., 2020), this strategy could result in a bias that appeared to be specific to VWM, but instead was mediated by a strategic allocation of attention. We tested this possibility in Experiment 2.

Experiment 2: Complex Color Memory Task

In Experiment 2 we investigated whether the results of Experiment 1 were driven by a strategic allocation of attention, rather than a more general tendency for VWM content to influence correspondence. Following Hollingworth et al. (2013a), we created sets of slightly different exemplars within the same color category, and tested memory for an exact color against a foil that was another member of the set. Ternus displays were created such that the colors could either match the color of a given element exactly or not (Figure 2B). Attending to specific Ternus elements in this experiment would be as likely to interfere with the memory trace

as it would be to refresh it, thereby eliminating the incentive to use such a strategy.

Method

Participants

A different group of 12 observers (mean age 23) from the same population and receiving the same compensation as those in Experiment 1 were tested in Experiment 2.

Stimuli

The stimuli were the same as in Experiment 1, with the exception that only three instead of four color categories were used, and for each there were four variations within the category, the original color as used in Experiment 1 and three more colors of the same color category. Specifically, the new colors were the following: turquoise 2 (RGB: 2, 140, 114; 21 cd/m^2); turquoise 3 (RGB: 1, 114, 140; 15 cd/m^2); turquoise 4 (RGB: 40, 98, 140; 12 cd/m^2); olive-green 2 (RGB: 132, 118, 1; 18 cd/m^2); olive-green 3 (RGB: 115, 132, 1; 21 cd/m^2); olive-green 4 (RGB: 88, 132, 3; 19 cd/m^2); salmon 2 (RGB: 242, 109, 80; 29 cd/m^2); salmon 3 (RGB: 242, 79, 113; 24 cd/m^2); and salmon 4 (RGB: 242, 109, 138; 31 cd/m^2). The Ternus displays were set up in the same way as in Experiment 1, except that the specific version of a color for a given element was selected randomly from among the four exemplars within a given color category (Figure 2B).

Task

The tasks were the same as in Experiment 1.

Procedure

The procedure was the same as in Experiment 1 with the exception that the longest ISI between Ternus frames was 160 ms, and therefore this was the ISI chosen for the demonstration of group motion in the beginning of the session. Due to differences in the design, 10 practice trials and 8 blocks of 50 experimental trials were presented. A break was provided every 25 trials.

Design

A 5 (Memory Color: EB-Match, GB-Match, Third-Match, No-Bias Match, No-Bias No-Match) × 2 (Color Type: Exact, Inexact) × 5 (Inter-Stimulus Interval: 0, 20, 40, 80, 160 ms) within-subjects design was used. The new variable in this experiment was Color Type. For those trials in which there was a match between the memory color and one or more of the Ternus elements, half of the time it was an exact match and the other have it was inexact (i.e., a different exemplar from the same color category). The factor ISI was reduced by one level in order to decrease the number of conditions. All factors were completely counterbalanced and randomly mixed within blocks of trials for a total of eight repetitions of the full design.

Data Analysis

We again calculated the mean error rates in the memory task for each participant and replaced participants who had an error rate higher than 25%, which resulted in the replacement of one participant. The mean error rate of the remaining participants was 13.88%. We also replaced a participant who showed a strong ISI

effect in all no-bias conditions that was in the opposite direction of that shown by all the other participants, and that we therefore believe accidentally inverted the response keys. Finally, trials with key presses other than the response keys (0.23%) and extreme long RTs (>8000 ms, 0.71%) were also eliminated as in Experiment 1.

Results and Discussion

The results were very similar to those of Experiment 1. Mean Group Motion responses are shown for the competitive-bias and no-bias conditions separately in Figure 5. We first conducted a 5 (Memory Color: EB-Match, GB-Match, Third-Match, No-Bias Match, No-Bias No-Match) × 2 (Color Type: Exact, Inexact) × 5 (Inter-Stimulus Interval: 0, 20, 40, 80, 160 ms) repeated-measures ANOVA on individual mean group motion responses. It revealed a main effect of Memory Color, $F(4, 44) = 17.00$, $p < .001$, $adj.$ $\eta_p^2 = .57$, and an interaction between Memory Color and ISI, $F(16, 176) = 4.55$, $p < .001$, $adj.$ $\eta_p^2 = .23$, (no Greenhouse-Geisser correction possible), but no other significant interactions with Memory Color, $Fs < 1.66$, $p > .177$, $adj.$ $\eta_p^2 < .05$. Holms corrected paired t tests revealed that all levels of the factor Memory Color differed significantly from each other, $t(11) > 2.83$, $p_{holm} < .49$, $adj.$ $\eta_p^2 = .37$, with the exception of the comparison between the two no-bias display conditions, $t(11) = 1.05$, $p_{holm} = .636$, $adj.$ $\eta_p^2 = .008$, and the comparison between the EB-Match and the Third-Match condition, $t(11) = 1.01$, $p_{holm} = .636$, $adj.$ $\eta_p^2 = .002$.

To investigate the effect of working memory content in the two different display conditions, we next conducted separate analyses for each of them. Mean group-motion responses in the

competitive-bias display (Figure 5, left) were submitted to a 3 (Memory Color: EB-Match, GB-Match, Third-Match) × 2 (Color Type: Exact, Inexact) × 5 (Inter-Stimulus Interval: 0, 20, 40, 80, 160 ms) repeated-measures ANOVA. There was a main effect of ISI such that group motion responses increased moderately with ISI from 35% at an ISI of 0 ms to 48% at an ISI of 160 ms, $F(4, 44) = 5.66$, $p = .001$, $adj.$ $\eta_p^2 = .28$. In addition, there was a main effect of Memory Color, $F(2, 22) = 10.45$, $p = .001$, $adj.$ $\eta_p^2 = .44$, and a trend for the interaction between Memory Color and Color Type, $F(2, 22) = 2.66$, $p = .092$, $adj.$ $\eta_p^2 = .12$. None of the other interactions were significant, $F_s < 1.10$, $p > .370$, $adj.$ $\eta_p^2 < .008$. Follow-up comparisons confirmed that, as in Experiment 1, group motion responses were higher for the GB-Match condition (49%) than for the EB-Match condition (33%), $t(11) = 3.09$, $p_{holm} = .021$, $adj.$ $\eta_p^2 = .42$. They were also higher for the GB-Match condition (49%) than the Third-Match condition (30%), $t(11) = 3.91$, $p_{holm} = .007$, $adj.$ $\eta_p^2 = .54$. There was no reliable difference between the EB-Match and the Third-Match condition $t(11) = 1.01$, $p_{holm} = .334$, $adj.$ $\eta_p^2 = .002$. Given the trend of an interaction between Memory Color and Color Type, we conducted separate post hoc ANOVAs for each Color Type condition. The main effect of Memory Color was significant for both, the exact color type condition, $F(2, 22) = 8.29$, $p = .002$, $adj.$ $\eta_p^2 = .38$, and the inexact color type condition, $F(2, 22) = 10.09$, $p = .001$, $adj.$ $\eta_p^2 = .43$. The pattern of effects for exact color matches was the same as in the main analysis—with higher group responses in the GB-Match (51%) condition than the EB-Match (30%) condition, $t(11) = 3.16$, $p_{holm} = .021$, $adj.$ $\eta_p^2 = .43$, and higher group responses in the GB-Match condition (51%) than in the Third-

Figure 5
Results of Experiment 2: Mean Percent of Group Motion Responses as a Function of ISI, Memory Color and Color Type (Left Graph) or ISI and Color Match (Right Graph)
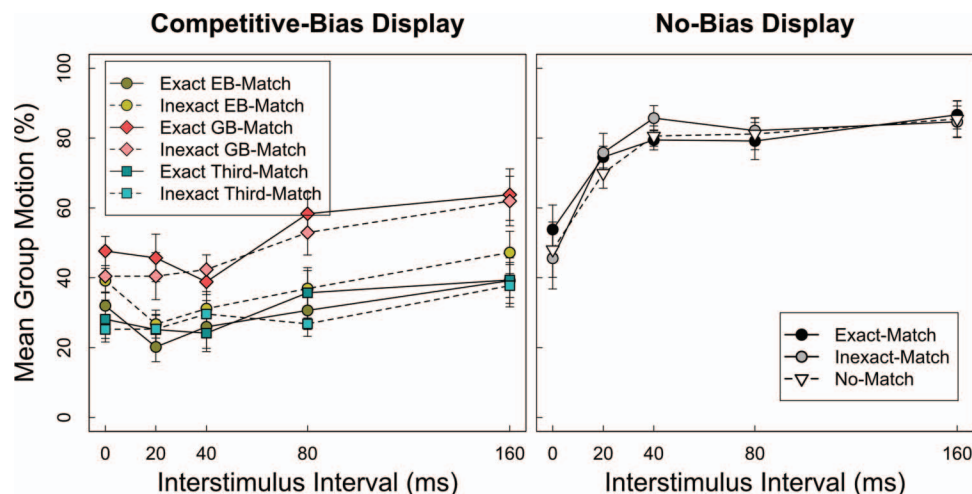
Note. The left graph shows the competitive-bias display condition for each of the three memory color conditions, element bias match (EB-Match), group bias match (GB-Match), and third color match (Third-Match) for each color type condition (exact and inexact color match). The right graph represents the no-bias display condition for each of the three color match conditions, the memory color either matching the element's color exactly (Exact-Match) or inexactly (Inexact-Match), or not at all (No-Match). Standard errors represent within-subject SEs after Cousineau-Morey (Cousineau, 2005; Morey, 2008). ISI = interstimulus interval. See the online article for the color version of this figure.

Match condition (31%), $t(11) = 3.31$, $p_{holm} = .021$, *adj.* $\eta_p^2 = .45$, but no significant difference between the EB-Match and the Third-Match conditions, $t(11) = -0.19$, $p_{holm} = .850$, *adj.* $\eta_p^2 = -.09$. For the inexact color type condition, on the other hand, the only significant difference was between the GB-Match (48%) and Third-Match (29%) condition, $t(11) = 4.12$, $p_{holm} = .005$, *adj.* $\eta_p^2 = .57$, though there were trends for the other two comparisons: GB-Match (48%) versus EB-Match (36%), $t(11) = 2.49$, $p_{holm} = .060$, *adj.* $\eta_p^2 = .30$, and EB-Match (36%) versus Third-Match (29%), $t(11) = 2.18$, $p_{holm} = .060$, *adj.* $\eta_p^2 = .24$. Overall then, the exact match conditions of Experiment 2 replicated the pattern of data observed in Experiment 1, and the inexact match condition yielded a weaker version of this pattern.

Next, mean group-motion responses in the no-bias display condition (Figure 5 right) were submitted to a 3 (Color Match: Exact-Match, Inexact-Match, No-Match) × 5 (Inter-Stimulus Interval: 0, 20, 40, 80, 160 ms) repeated-measures ANOVA. There was a main effect of ISI, $F(4, 44) = 10.61$, $p = .002$, *adj.* $\eta_p^2 = .44$, with group motion responses ranging from 49% for the 0-ms ISI to 86% for the 160-ms ISI. There was no significant effect of Color Match, $F(2, 22) = 0.29$, $p = .749$, *adj.* $\eta_p^2 = -.063$, and no interaction between the two factors, $F(8, 88) = 0.75$, $p = .645$, *adj.* $\eta_p^2 = -.021$.

The results of Experiment 2 replicated the patterns observed in Experiment 1. More group motion was reported when the memory color matched elements in the Ternus display that biased group motion (GB-Match condition) than when it matched elements that biased element motion (EB-Match). This was true even though there was no incentive to attend to elements that matched the memory color. In addition, exact memory matches seemed to be more effective than inexact matches, as the post hoc comparisons showed significant effects between the GB-Match and the EB-Match conditions only for the exact matches, but not for the inexact matches. Although this must be interpreted with caution because the initial interaction between Memory Color and Color Type in the competitive display was not significant, it is reminiscent of a recent study showing that the motion history of elements in Ternus displays can bias correspondence, but only if the type of historical motion (i.e., smooth vs. apparent) matches that of the Ternus display (Stepper, Moore, et al., 2020b). This suggests that the representations of the objects held in memory need to match the visible stimuli very closely in order to have an effect on correspondence. That is, the comparison operation appears to be quite specific. Future research can systematically manipulate the magnitude of feature differences to more precisely characterize the relationship between correspondence and feature similarity.

Experiment 3: Size Memory Task With Color Being Incidental

In Experiment 3, we examined the generality of the effect of VWM content on correspondence processes. In particular, we asked whether VWM content that is incidental to the explicit memory task can also impact correspondence, or alternatively, if it is only the information that is being held active in the service of the current task that influences correspondence. The memory task was changed to report the size of a rectangle rather than its color (see Hollingworth & Luck, 2009). The rectangle, however, happened to be a particular color that did or did not match some of the elements of the Ternus displays, but participants were not asked to remember the color and were not tested on it. The question was whether the color, incidentally encoded along with the size of the rectangle, would bias Ternus motion. If it did, then it would confirm that even incidentally encoded content is factored into the correspondence process. By way of preview, incidental color did not bias the perception of Ternus motion.

Method

Participants

A different group of 12 observers (mean age 23) from the same population and receiving the same compensation as those in Experiments 1 and 2 were tested in Experiment 3.

Stimuli

The Ternus display was exactly the same as in Experiment 1. For the memory task, the to-be-remembered stimulus was a rectangle that varied in size from 1.76° and 2.91° (randomly selected). The color of the rectangle was one of the four colors used in Experiment 1, and color-match to the Ternus display was defined in the same way as in Experiment 1. At the end of the trial, two squares were presented, one that was the same size as the original to-be-remembered square (target) and one that was 0.62° smaller or 0.62° larger than the target square (foil). Both squares were the same color as the original square. The sides of the target and foil were selected randomly on each trial.

Task

The Ternus task was exactly the same as in Experiments 1 and 2. For the memory task, participants indicated which of two rectangles, the left or the right, matched the size of the rectangle presented at the beginning of the trial.

Procedure and Design

The procedure and design were the same as in Experiment 1.

Data Analysis

As in the previous two experiments, we calculated the mean error rates in the memory task for each participant and replaced participants with error rates higher than 25% (five participants). The mean error rate of the remaining participants was 14.12%. Trials with key presses other than the response keys (0.13%) and extreme long RTs (>8000 ms, 0.15%) were also eliminated, as in the previous experiments.

Results and Discussion

Mean Group Motion responses are shown for competitive-bias and no-bias displays separately in Figure 6. We first conducted a 2 (Display: competitive-bias, no-bias) × 4 (Memory Color: EB-Match, GB-Match, Third-Match, No-Match) × 6 (ISI: 0, 20, 40, 80, 160, 300 ms) repeated-measures ANOVA on individual mean group motion responses. In contrast to Experiment 1, there was no main effect of Display, $F(1, 11) = 1.24$, $p = .289$, *adj.* $\eta_p^2 = .02$, no interaction between Display and Memory Color, $F(3, 33) = 1.29$, $p = .294$, *adj.* $\eta_p^2 = .02$, and no three-way interaction among all three factors, $F(15, 165) = 0.93$, $p = .534$, *adj.* $\eta_p^2 = -.006$.

Figure 6
Results of Experiment 3: Mean Percent of Group Motion Responses as a Function of ISI and the Memory Color
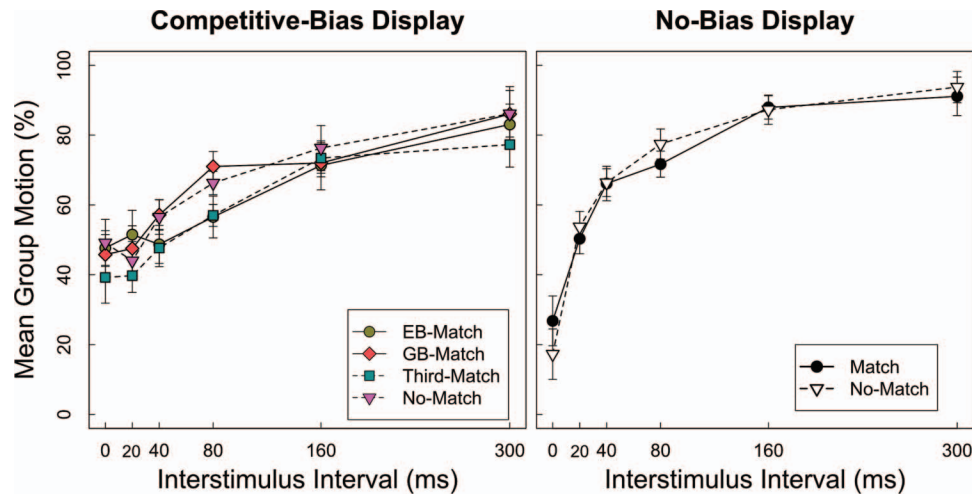
Note. The left graph shows the competitive-bias display condition for each of the four memory color match conditions, element bias match (EB-Match), group bias match (GB-Match), third element color match (Third-Match) or no element color match (No-Match). The right graph represents the no-bias display condition, the Memory Color either matching the element's color (Match) or not (No-Match). Standard errors represent within-subject SEs after Cousineau-Morey (Cousineau, 2005; Morey, 2008). ISI = interstimulus interval. See the online article for the color version of this figure.

There was, however, an interaction between Display and ISI, $F(5, 55) = 11.80, p < .001, adj. \eta_p^2 = .47$.

To allow for comparison with Experiment 1 and to investigate the effect of working memory content, we conducted separate analyses for the two display conditions. Individual mean group responses for the competitive-bias display (Figure 6, left) were submitted to a 4 (Memory Color: EB-Match, GB-Match, Third-Match, No-Match) $\times$ 6 (ISI: 0, 20, 40, 80, 160, 300 ms) repeated-measures ANOVA. There was a main effect of ISI, $F(5, 55) = 10.25, p = .002, adj. \eta_p^2 = .44$, such that group motion responses increased from 45% at the 0 ms ISI to 83% at the 300 ms ISI. There was, however, no effect of Memory Color, $F(3, 33) = 2.51, p = .130, adj. \eta_p^2 = .11$, and no interaction between Memory Color and ISI, $F(15, 165) = 1.01, p = .452, adj. \eta_p^2 = .0008$.

Next, mean group-motion responses in the no-bias display condition (Figure 6, right) were submitted to a 2 (Memory Color: Match, No-Match) $\times$ 6 (Inter-Stimulus Interval: 0, 20, 40, 80, 160, 300 ms) repeated-measures ANOVA. There was a significant effect of ISI, $F(5, 55) = 30.91, p = .001, adj. \eta_p^2 = .71$, such that group motion responses increased from 22% at the 0 ms ISI to 92% at the 300 ms ISI. We found no significant effect of Memory Color, $F(1, 11) = 0.02, p = .900, adj. \eta_p^2 = -.09$, but a trend for an interaction between ISI and Memory Color, $F(5, 55) = 2.18, p = .070, adj. \eta_p^2 = .09$. Separate post hoc comparisons at each level of ISI, however, showed no significant effect of Memory Color for any level of ISI, $-1.33 < = t(11) < = 1.62, p > = .133, adj. \eta_p^2 < = 0.12$.

In summary, unlike in Experiments 1 and 2, colors held in VWM did not bias correspondence in Ternus displays. The difference between this experiment and the previous two is that participants were not required to explicitly encode color. As-

suming that color was incidentally encoded when memorizing the size of the to-be-remembered square, then there is no evidence that this incidental memory content interacts with the correspondence process. We do not have a separate measure of whether or not color was encoded, and so we cannot rule out the possibility that it was not. However, previous studies using this general strategy in the context of asking whether incidentally encoded color information can interact with attentional guidance found that it did (Hollingworth & Bahle, 2020; Hollingworth & Luck, 2009; Hollingworth et al., 2013a, 2013b; but see Olivers et al., 2006). Participants in the study by Hollingworth and Bahle (2020), for example, had to remember the size of a colored item, exactly as in our study. They then had to search an array for an object with a certain target feature (the orientation of a "c"). The color of the object could match that of the item memorized or not. Participants were faster to detect the target on the object when its color matched the memory color than when it did not, despite the memory color being incidental and completely irrelevant to the task. Similar effects of incidental memory features influencing visual search have been shown for different types of search tasks, different dependent measures, and different memory and stimulus feature dimensions (Bahle et al., 2018; Foerster & Schneider, 2018; Hollingworth & Luck, 2009; Hollingworth & Matsukura, 2019; Hollingworth et al., 2013a, 2013b). We have little reason to suspect, therefore, that color was not similarly incidentally encoded in this experiment. Note also that biasing effects from incidental features in VWM have been most consistently observed in paradigms probing oculomotor orienting, a measure that is particularly sensitive to VWM-based guidance (Bahle et al., 2018).

General Discussion

This study investigated the influence of VWM content on correspondence processes using Ternus motion. Prior to viewing competitive-bias Ternus displays (Figure 1C), observers were shown a color to commit to memory for later report. When the memory color matched the element-bias color, more element motion was reported, whereas when the memory color matched the group-bias color, more group motion was reported (Experiments 1 and 2). These results confirm that VWM content can contribute to correspondence as expected given the assertion that the function of correspondence is to support continuous representations of objects in the world even when they become invisible. In Experiment 3, information that was only incidental to the explicit memory task failed to influence Ternus motion. Assuming that the information was maintained in VWM, this result indicates a limitation of the impact of VWM content on correspondence processes that further studies could confirm and explore.

The current findings contribute to a broader literature in which various perceptual processes have been shown to be influenced by information beyond that which is immediately present in the image. Perceptual grouping of elements within static displays, for example, has been shown to be influenced by past experience (e.g., Kimchi & Hadad, 2002; Vecera & Farah, 1997; Vickery & Jiang, 2009). Figure–ground perception is influenced by familiarity (e.g., Cacciamani et al., 2014; Peterson & Gibson, 1994a, 1994b). Semantic attributes of stimuli can influence dominance in the competition for awareness in binocular rivalry (e.g., Alpers & Pauli, 2006; Anderson et al., 2011; Paffen et al., 2011; Sheth & Pham, 2008), as can VWM content (Scocchia et al., 2014) and attention (e.g., see Dieter & Tadin, 2011; Paffen & Alais, 2011 for reviews). And finally, most directly comparable to the current work, are demonstrations of memory content influencing perceptual ambiguities in dynamic displays, including VWM content biasing perceptions of bistable shape-from-motion displays (Scocchia et al., 2013) and long-term semantic memory content influencing apparent motion (Chen & Zhou, 2011; Hsu et al., 2015; Ramachandran et al., 1998; Tse & Cavanagh, 2000; Yu, 2000). The current work brings together many of the design features of those previous studies and adds to them by providing insight into higher-level influence on object correspondence processes, in particular, as the ambiguity in Ternus motion, unlike the ambiguity in, for example, binocular rivalry and figure-ground perception, seems to concerns correspondence processes at higher level of processing (Hein & Moore, 2014; Stepper, Moore, et al., 2020a; see also Moore et al., 2020, for the distinction between motion and object correspondence).

One important question regarding perceptual biasing effects of the sort reported here and those just reviewed is to what extent, if any, are they mediated by the orienting of attention to a specific (Ternus) element? Any given bias effect might reflect a direct influence of the biasing factor on the process in question. In the case of the current study, for example, that would be a direct effect of activating a feature in visual working memory enhancing the perception of one set of elements over another, thereby influencing correspondence. Alternatively, a given bias effect might reflect an indirect effect via attentional orientation. In the case of the current study, for example, it is possible that holding a given feature in VWM caused attention to be guided to the Ternus element of that

color, as it is known to do (Olivers et al., 2006; Soto et al., 2005), which in turn might have biased correspondence in the Ternus display, as it is also known to do (Stepper, Rolke, et al., 2020). The current study cannot discriminate between these alternatives. It is important to note, however, that if the impact of VWM content on the perception of Ternus motion is mediated by attention, it is not due to a strategic allocation of attention that is peculiar to the details of the current experiments. That possibility was ruled out in Experiment 2. Rather, it would reflect an important mediating relationship between attention and correspondence processes, a relationship that is an important question for further research.

In summary, the current study builds on earlier work testing the range of factors that determine object correspondence. In addition to spatiotemporal coherence and feature similarity—both image level and perceived—between stimuli, we have confirmed that VWM content contributes to correspondence processes. This is a significant addition to our understanding, because the feature information that is held in VWM is only mentally represented and not directly available in the image at the time that correspondence is established. It is, therefore, the kind of information that a system whose function it is to maintain the continuity of object representations across time and space would need to rely on (e.g., Hollingworth et al., 2008). There remain open questions regarding exactly what aspects of VWM content can influence correspondence. We found that incidentally encoded information did not, but there is much to be explored in this regard. We also do not know exactly what role attention plays in this process. We do know, however, that correspondence can be resolved on the basis of information that exists only in the viewer's memory and that it does so even when that information is irrelevant to that task.

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