1	Visual working memory content influences correspondence processes
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22	Word Count: 7747
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Abstract

26 Representing objects as continuous across time requires the establishment of 27 correspondence, whereby current stimuli are represented as deriving from the same 28 object as earlier stimuli. Spatiotemporal continuity and surface-feature similarity play 29 important roles in these correspondence processes. Because objects are often 30 represented across extended periods of time, visual working memory (VWM) content 31 should also play a role in object correspondence. We tested this prediction using Ternus 32 motion. Displays consisted of three-disk arrays that shifted horizontally by one position 33 between frames. Depending on how correspondence is resolved, Ternus displays are 34 perceived as group motion, where all three disks appear to move together, or element 35 motion, where one disk appears to jump across the others. Reports of which motion is 36 perceived provide an index of how correspondence was resolved. Ternus displays were 37 adapted such that the color of some disks biased element motion while the color of 38 others biased group motion. Maintaining one or the other of the colors in VWM for later 39 report systematically biased which type of motion was perceived (Experiments 1 and 2). 40 When color was incidental to the VWM task, however, it did not (Experiment 3). These 41 results confirm that VWM content contributes to object correspondence.

42 *Word Count: 198*

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

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Public Significance Statement

50	When an object moves, it can disappear or change appearance due to spurious changes
51	like lighting conditions, and yet we perceive it as a stable entity that exists continuously
52	over time. This is an achievement that artificial vision systems struggle to master. The
53	current study demonstrates that specific attributes that we hold in memory can
54	systematically influence how the visual system determines which objects belong
55	together across space and time, but only when the attributes are relevant to the current
56	task. This research expands our understanding of how the human visual system
57	represents objects as continuous over time, knowledge that could be used improve
58	artificial vision systems.
59	Word Count: 107

Visual working memory content influences correspondence processes

62 A central function of the visual system is to establish and maintain representations 63 of objects that are continuous over time. It does this despite movements of the objects 64 and movements of images of the objects on the retina due to head, body, and eye 65 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 66 67 (e.g., when a friend gets a new hair cut). The problem, which was referred to originally 68 in the motion perception literature as the correspondence problem (Ullman, 1979), has 69 been characterized by Dawson and colleagues as the problem of knowing "what went 70 where?" (Dawson, 1991). The idea is that objects in the world exist over time and space, 71 and they can project different images at different times, including no image at all when 72 an object is out of view for brief periods of time, as when it moves behind other objects. 73 For example, when your child is on a carousel and disappears out of sight on her way 74 around the pole, you perceive her as moving behind the pole, not as disappearing 75 momentarily and reappearing later. Objects, more generally, continue to exist over even 76 longer periods of time than this example, as when friends don't see each other for weeks 77 and yet are able to easily recognize each other when they meet again. Despite 78 discontinuous visual input, we can and do represent objects as continuous entities, and 79 we update their representations on the basis of new information when it becomes 80 available. The correspondence problem is the question of how the visual system comes 81 to associate newly available visual information with the "correct" existing object 82 representation, rather than with another object representation, or with no object 83 representation at all, thereby requiring the establishment of a new object representation.

84 The "problem" part of the correspondence problem is the question of on what 85 basis correspondence is established. Two broad hypotheses have dominated the 86 literature. According to the spatiotemporal priority hypothesis, correspondence is based 87 on spatiotemporal information (e.g., Flombaum et al., 2012; Pylysyn, 2001; Scholl, 88 2001). The idea is that if the temporal and spatial relations between two stimuli are 89 consistent with the mechanics of how a physical object could move (or remain 90 stationary) over time, then correspondence will be established, and a single object will 91 be perceived, with the two stimuli reflecting different states of that object. The 92 strongest version of this hypothesis asserts that featural differences other than 93 spatiotemporal factors, such as color and shape, are irrelevant. Under this view, if other 94 features are different when correspondence is established based on spatiotemporal 95 coherence, then the difference will be accommodated, such as when an object is 96 perceived as morphing in shape when apparent motion is perceived between two 97 differently shaped stimuli that are presented in quick succession at nearby locations 98 (Burt & Sperling, 1981; Navon, 1976; Navon 1983; Kolers & Pomerantz, 1971; Kolers 99 & von Grünau, 1976). The alternative hypothesis to spatiotemporal priority asserts that 100 although spatiotemporal coherence plays a significant role in establishing 101 correspondence, so do the features of objects, such as color and shape. Under this view, 102 correspondence is resolved on the basis of whatever balance of information provides the 103 least ambiguous solution to the correspondence problem (Hein & Cavanagh, 2012; Hein 104 & Moore, 2012; Hein & Moore, 2014; Hollingworth & Franconeri, 2009; Hollingworth 105 & Matsukura, 2019; Richard et al., 2008). 106 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

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108	with the parting-friends example (e.g., Riesenhuber & Poggio, 1999). But at this point
109	there is also substantial evidence that surface features are used to resolve
110	correspondence across short stimulus intervals as well, and can even dominate
111	spatiotemporal factors. Much of that evidence comes from experiments using some
112	form of ambiguous apparent motion to test what factors tip the balance in favor of one
113	percept or another (e.g., Ullman, 1979: Burt & Sperling, 1981; Dawson et al., 1994;
114	Green, 1986; Hein & Moore, 2012; Shechter et al., 1988; von Schiller, 1933). Ternus
115	motion is an example (Pickler, 1917; Ternus, 1926). In a Ternus display, an array of
116	(usually) three adjacent elements is presented in alternation with the same set of
117	elements shifted by one position (Figure 1A). In this ambiguous motion display the
118	elements can be perceived as moving all together (group motion) or as one element
119	jumping across the other two which remain stationary (element motion). Notice that the
120	two different perceptions of Ternus displays-group motion versus element motion-
121	imply mutually exclusive alternative solutions to the correspondence problem.
122	Therefore, which type of motion is reported can be used as a measure of how
123	correspondence was resolved under a given set of conditions. A strong determinant of
124	whether group or element motion is perceived, and by inference therefore how
125	correspondence is resolved, is the time between the two displays, or the interstimulus
126	interval (ISI). Specifically, at long ISIs, group motion tends to be perceived, whereas at
127	short ISIs, element motion tends to be perceived (e.g., Breitmeyer & Ritter, 1986;
128	Petersik & Pantle, 1979). Because ISI is a spatiotemporal variable, the fact that the
129	perception of Ternus motion depends on it is consistent with the spatiotemporal priority
130	hypothesis. It has also been shown, however, that whether group or element motion is
131	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 & 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).

138 Given that surface features can influence correspondence as strongly as 139 spatiotemporal coherence does, a further question is what level of surface feature 140 representation is critical (He & Nakayama, 1994; Hein & Moore, 2014; Stepper et al., in 141 press)? Is it the similarity of features as they exist in the image itself, such as luminance, 142 image size, and image shape, or is it the similarity of features as they are abstracted 143 from the image to represent objects in the world, such as perceived reflectance (i.e., 144 *lightness*), perceived size, and perceived shape, which are representations that discount 145 differences in apparent illumination and depth? This question was addressed by adding 146 regions of apparently different illumination conditions and occluding surfaces to Ternus 147 displays, which provided separate assessments of the impact of perceived features and 148 image-level features on object correspondence (Hein & Moore, 2014; see also Palmer et 149 al., 1996; Rock & Brosgale, 1964; Rock et al., 1992 for this strategy applied to 150 perceptual grouping in static displays). This and related work showed that 151 correspondence is influenced not only by the luminance, image size and image shape of 152 elements across frames, but also by the perceived lightness, perceived size, and 153 perceived shape of elements (He & Nakayama, 1994; Hein & Moore, 2014; Stepper et 154 al., in press).

155 The aim of the current work was to extend this line of questioning to ask whether 156 Ternus motion can be biased on the basis of visual working memory (VWM) content, 157 which is based on feature information that is not present in the image at the time that 158 correspondence is established. The function of object correspondence is to support the 159 representation of objects as entities in the world that exist over time, even when they are 160 not visible for periods of time. For example, it has been proposed that object 161 correspondence across the perceptual gap created by a saccade depends on VWM 162 (Hollingworth et al., 2008), and manipulations of VWM have been shown to bias this 163 correspondence operation (Hollingworth & Luck, 2009). It follows, therefore, that 164 information in memory should be capable of contributing to the correspondence process 165 in the perception of motion. To test this prediction, we added a working memory task to 166 competitive-bias Ternus displays (Hein & Schütz, 2019; Stepper, Rolke et al., 2020) and 167 asked whether the content held in VWM would systematically bias which type of 168 motion was perceived. The strategy is analogous to that used to test whether VWM 169 content biases the control of visual attention (e.g., Soto et al., 2005; Olivers et al., 170 2006).

171 Figure 1C illustrates a competitive-bias Ternus display. The elements differ in 172 color such that one color is consistent with element motion and inconsistent with group 173 motion, while another color is consistent with group motion and inconsistent with 174 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 175 176 element-bias color, or neither (see Figure 2A). We found that reports of group or 177 element motion were systematically biased by these color matches (Experiment 1). We 178 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).



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186 Figure 1. Different types of Ternus displays. A. Standard no-bias display in which all items are the same color. In this display correspondence is influenced by the Inter-187 188 stimulus Interval (ISI), for short ISIs element motion is seen (upper), for long ISIs 189 group motion is seen (lower). B. In a simple feature-bias display, the Ternus elements 190 have different colors, being consistent with either element motion (upper) or group 191 motion (lower), leading to the corresponding motion percepts being seen more 192 frequently. C. In the competitive-bias display, one color of the Ternus elements is 193 consistent with element motion and inconsistent with group motion (here turquoise), 194 while another color is compatible with group motion and inconsistent with element 195 motion (here salmon). Percepts in this display tend to be independent of ISI and 196 maximally ambiguous.

Experiment 1: Simple color memory task

198 At the beginning of each trial, subjects were shown a colored rectangle and 199 asked to remember the color. Next, a Ternus display was presented with either 200 competitive-bias displays (Figure 1C; half of the trials) or no-bias displays (Figure 1A; 201 other half of the trials). Figure 2A illustrates the conditions. For competitive-bias 202 displays, the memory color could match one of the three colors, the group-bias color 203 (GB-Match), the element-bias color (EB-Match) or the third color (Third-Match), or it 204 could match none of the colors in the Ternus display (No-Match). The hypothesis is 205 that activating a given color as a trace in VWM will enhance the processing of elements 206 of that color in the competitive Ternus display, thereby biasing the type of motion that 207 this color is consistent with. We expected, therefore, to find more group motion reports 208 in the condition in which the memory color matched the group-bias color compared to 209 the element-bias color condition. As a control we also used no-bias displays, in which 210 the memory color either matched the elements in the Ternus displays (Match) or did not 211 (No-Match). We did not expect memory color to influence correspondence in this case, 212 as all the elements were identical and thus correspondence should be based on the ISI 213 between Ternus frames.

214 Methods

Participants. 12 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-tonormal visual acuity and color vision. Choice of sample sizes were 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 alpha of .05. To be conservative, we therefore planned a sample size of 12
for each of the experiments reported here.

- 226 *Equipment*. Stimuli were presented using a PC with Windows XP driving a 17-inch
- color monitor with a spatial resolution of 1024 x 768 and a refresh rate of 100 Hz. The

228 experiment was controlled with MATLAB software (version 7.4 release 2007a,

229 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

231 conducted in a dimly lit individual testing room.

232 Stimuli. The memory color was a 1.50° square presented at the center of the monitor. It 233 was one of four photometrically equiluminant colors: turquoise (RGB: 0, 140, 140; 22 234 cd/m²), olive-green (RGB: 132, 132, 0; 22 cd/m²), pink (RGB: 225, 10, 225; 22 cd/m²) 235 and salmon (RGB: 142, 67, 67; 22 cd/m²). Ternus displays consisted of two frames of 236 three circular elements (1.50° diameter), presented sequentially with a variable ISI 237 between them. The elements in a given frame were separated center-to-center by 1.50° 238 and shifted one position to the right across the two frames. These displays were 239 presented such that the four element positions of the combined first and second frame 240 were centered horizontally, 1.32° above a central fixation cross (0.26° x 0.26°). For no-241 bias displays all of the elements were displayed in one of the four colors. For 242 competitive-bias displays, the three Ternus elements were presented in different colors, 243 as illustrated in Figure 1C. The middle elements in the first and second Ternus frames 244 were the same color. The outer two elements in the two frames were the same color as

245 each other, but were a different color from the middle elements. And finally, the last 246 element in the first frame and the first element of the second frame were also the same 247 color as each other, and different from the other two pairs of elements. Which color was 248 used for which element pair was selected randomly. This configuration established two 249 competing color biases. Specifically, the color of the middle elements creates a match 250 that is consistent with group motion, and inconsistent with element motion, whereas the 251 color of the two outer elements creates a match that is consistent with element motion 252 and inconsistent with group motion. The third color match is consistent with neither 253 group nor element motion. Finally, following the Ternus display on each trial, two 254 colored 1.50° squares were presented 2.80° to the left and right of fixation. One square 255 (its left or right position randomly selected) was the same color as the square presented 256 at the beginning of the trial (target), and the other square was a different color, 257 randomly chosen among the three remaining colors (foil).





259 Figure 2. Illustration of memory color conditions used the three experiments. A. 260 Experiment 1 & 3: In the competitive-bias display condition, the memory color can either match the element bias compatible color (here olive-green), the group bias 261 262 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 263 either match the color of the Ternus elements (here turquoise) or not. **B.** Experiment 2: 264 265 The same competitive-bias and no-bias Ternus conditions were used as in Experiment 266 1&3. The color match could, however, either be an exact match or not, the memory 267 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 oneof the colors of the other two color categories.

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270 *Task.* At the end of the trial, participants first reported whether they perceived group or 271 element motion using the "j" and "f" keys on the computer keyboard, respectively. 272 Next, the memory probe display was presented, and participants indicated whether the 273 left or the right rectangle was the same color as the rectangle presented in the beginning 274 of the trial, using the "j" and "f" keys, respectively.



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276 Figure 3. Trial sequence of Experiment 1. In the beginning of the trial a fixation cross 277 was presented for 800 ms followed by a blank screen for 500 ms (not illustrated). Then 278 participants had to memorize the color of the rectangle presented at the center of the 279 screen (Color memorization). Next the Ternus display was presented. In the end of the 280 trial participants had to indicate which type of Ternus motion they saw (Answering 281 period), followed by a blank interval for 500 ms or an error message if a non-response 282 key was pressed (not illustrated). Finally, after another fixation interval of 800 ms two 283 differently colored rectangles were presented and participants had to indicate which 284 rectangle had the same color as the memory probe of the beginning of the trial. If 285 necessary an error feedback was given (not illustrated).

286 Procedure. Participants were tested individually in single 50-minute sessions. They first 287 read and signed an informed consent form in accordance with the ethical guidelines of 288 the declaration of Helsinki (World Medical Association, 2013). After written 289 instructions on the computer screen, participants were shown two examples of a no-bias 290 Ternus display in which observers usually perceive element motion (the shortest ISI 291 between Ternus frames presented during the experiment: 0 ms ISI) and group motion 292 (the longest ISI between Ternus frames presented during the experiment, 300ms). The 293 Ternus display was first presented as cycling continuously to give the observer more 294 time to see the motion. After that a one-cycle version was presented as in the 295 experiment itself. After 16 practice trials of initial familiarization with the different 296 displays, participants completed 8 blocks of 48 experimental trials each. A break was 297 provided every 24 trials.

298 Trial events are illustrated in Figure 3. Each trial began with the fixation cross for 299 800 ms. Following a 500 ms blank interval, the memory color was presented for 300 300 ms, followed by a 1200 ms blank interval. The fixation cross and the first Ternus frame 301 were then presented for 200 ms, followed by a variable ISI between 0 and 300 ms and 302 the second Ternus frame for another 200 ms. The fixation cross remained on the screen 303 until a key press was recorded. If a key other than the "j" or "f" was pressed, a written 304 error message was presented for 1000 ms, otherwise a blank screen was presented for 305 500 ms. The fixation cross was then presented again for 800 ms, followed by the 306 memory-probe display until a keypress was made. A tone with frequency of 1200 Hz 307 for 200 ms and a written feedback for 1000 ms was provided if the foil was selected 308 instead of the target, or if any key other than the two response keys was pressed. After a 309 1000 ms inter-trial interval, the fixation cross for the next trial was presented.

310 Design. A 4 (Memory Color: EB-Match, GB-Match, Third-Match, No-Match) × 2

311 (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.

317 Data analysis: We planned to replace participants who had a mean error rate in the 318 memory task higher than 25%. No participant met this criterion in Experiment 1. The 319 mean error rate across participants was 7.23 %. Trials with key presses other than the 320 response keys (0.28 %) and extremely long RTs (> 8000 ms, 0.04 %) were eliminated. 321 For our analyses of variance (ANOVAs), Greenhouse-Geisser corrections were 322 used to account for violations of the sphericity assumption when they occurred. Alpha 323 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-324 325 squared that adjusts for the known positive bias in that measure (Mordkoff, 2019). All 326 analyses were done using R (R Development Core Team, 2008).

327 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: competitivebias, 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 groupmotion 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

335 ISI,
$$F(5,55) = 2.47$$
, $p = .096$, $adj.\eta_p^2 = .11$, and no three-way interaction, $F(15,165) = 0.92$, $p = .544$, $adj.\eta_p^2 = -.01$.

337 We next conducted separate analyses for the two display conditions. Individual 338 mean group responses for the competitive-bias display (Figure 4, left) were submitted to 339 a 4 (Memory Color: EB-Match, GB-Match, Third-Match, No-Match) × 6 (ISI: 0, 20, 40, 340 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) =341 12.41, p = .001, $adj.\eta_p^2 = .49$, and there was no interaction between Memory Color and 342 ISI, F(15,165) = 1.24, p = .246, $adj_{i}n_{p}^{2} = .02$. Follow-up comparisons confirmed what is 343 344 apparent in the figure. Group-motion reports were significantly higher in the GB-Match 345 condition (57%) than in the EB-Match condition (42%), t(11) = 3.58, $p_{\text{holm}} = .016$, $adj.\eta_p^2 = .50$. In addition, they were higher in the No-Match condition (54 %) than in 346 the EB-Match condition (42 %), t(11) = 3.74, $p_{holm} = .016$. $adj.\eta_p^2 = .52$. Finally, group 347 348 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 349 condition (54 %) compared to the Third-Match condition (42 %), t(11) = 4.68, p = .004, 350 351 $adj.\eta_p^2 = .64$. The remaining two comparisons between the GB-Match and the No-352 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 353 354 examined the effect of the ISI in more detail by analyzing each Memory Color condition 355 separately. We found a significant effect of the ISI in the GB-Match condition, F(5, 55)356 = 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) = 0.47, p = .799, p = .357

358 55) = 2.28,
$$p = .122$$
, $adj.\eta_p^2 = .10$, and No Match $F(5, 55) = 0.31$, $p = .776$, $adj.\eta_p^2 = -$
359 .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, $adj.\eta_p^2 = -.06$.



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Figure 4. Experiment 1: Mean percent of group motion responses as a function of ISI 369 370 and Memory Color. The left graph shows the competitive-bias display condition for 371 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 372 right graph represents the no-bias display condition for each of the two memory color 373 374 conditions, either matching the element's color (Match) or not (No-Match). Standard 375 errors represent within-subject SEs after Cousineau-Morey (Cousineau, 2005; Morey, 376 2008).

377 The results from Experiment 1 demonstrate that visual working memory content 378 can bias correspondence as revealed by the perception of Ternus motion: those elements 379 whose color matched the color being held in visual working memory dominated the 380 type of motion perceived. Specifically, when the memory color matched the group-bias 381 color, more group motion was perceived, and when it matched the element-bias color, 382 less group motion was perceived. The results from the no-bias display were also as 383 expected. Without any competing feature information, correspondence, and the resulting 384 perception of group versus element motion, was influenced only by ISI such that more 385 group motion was perceived at longer ISIs (e.g., Petersik & Pantle, 1979; Pikler, 1917; 386 Ternus, 1926). Moreover, we also found an influence of the type of display 387 (competitive-bias vs. no-bias) on the strength of the ISI effect: When feature 388 information was conflicting with regard to the correspondence of elements across 389 frames of motion in the competitive-bias displays, ISI had a less strong effect on 390 whether group or element motion was perceived compared to the no-bias display. In 391 addition, the ISI had an effect when the memory color matched the group bias as 392 compared to the element bias (or third color). The lack of an effect of ISI in the 393 competitive-bias display without any additional bias (No-Match condition) has been 394 shown before (Stepper et al., 2020), and is consistent with the assertion that feature 395 information, which favors neither group nor element motion in the case of competitive-396 bias displays, can influence Ternus motion as strongly as ISI does. More mysterious is 397 the finding that there was a small effect of the ISI when the memory color matched the 398 group bias. We can only speculate as to what the reason for this difference is. One 399 possibility is that a correct feature mapping in the element bias case could be maintained 400 if in addition to the first element jumping over the other two, the two middle elements

401 appeared to swap places, a solution that might have satisfied the visual system at any
402 ISI. In contrast, in the case of the group bias such a perfect mapping is impossible
403 leaving some room for the effect of the ISI to determine the response as well. Future
404 research should address this speculation by asking more specifically about the exact
405 percept the participants perceive.

406 It is possible that the influence of VWM content in this experiment reflects a 407 strategic use of colored elements in the Ternus displays to facilitate the memory task, 408 rather than a more general interaction between memory content and correspondence 409 processes. Specifically, it is possible that in order to refresh a memory trace, 410 participants strategically attended to elements of the same color. Because attending to 411 individual elements can influence how Ternus displays are perceived (Stepper, Rolke et 412 al., 2020), this strategy could result in a bias that appeared to be specific to VWM, but 413 instead was mediated by a strategic allocation of attention. We tested this possibility in 414 Experiment 2.

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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

- 423 as likely to interfere with the memory trace as it would be to refresh it, thereby
- 424 eliminating the incentive to use such a strategy.

425 Methods

426 *Participants*. A different group of 12 observers (mean age 23) from the same population

427 and receiving the same compensation as those in Experiment 1 were tested in

428 Experiment 2.

429 Stimuli. The stimuli were the same as in Experiment 1, with the exception that only 430 three instead of four color categories were used, and for each there were four variations 431 within the category, the original color as used in Experiment 1 and three more colors of 432 the same color category. Specifically, the new colors were the following: turquoise 2 433 (RGB: 2, 140, 114; 21 cd/m²); turquoise 3 (RGB: 1, 114, 140; 15 cd/m²); turquoise 4 434 (RGB: 40, 98, 140; 12 cd/m²); olive-green 2 (RGB: 132, 118, 1; 18 cd/m²); olive-green 3 (RGB: 115, 132, 1; 21 cd/m²); olive-green 4 (RGB: 88, 132, 3; 19 cd/m²); salmon 2 435 436 (RGB: 242, 109, 80; 29 cd/m²); salmon 2 (RGB: 242, 79, 113; 24 cd/m²); salmon 4 437 (RGB: 242, 109, 138; 31 cd/m²). The Ternus displays were set up in the same way as in 438 Experiment 1, except that the specific version of a color for a given element was 439 selected randomly from among the four exemplars within of a given color category 440 (Figure 2B).

441 *Task.* The tasks were the same as in Experiment 1.

442 *Procedure*. The procedure was the same as in Experiment 1 with the exception that the 443 longest ISI between Ternus frames was 160 ms, and therefore this was the ISI chosen 444 for the demonstration of group motion in the beginning of the session. Due to 445 differences in the design, 10 practice trials and 8 blocks of 50 experimental trials were446 presented. A break was provided every 25 trials.

447 Design. A 5 (Memory Color: EB-Match, GB-Match, Third-Match, No-Bias Match, No-448 Bias No-Match) \times 2 (Color Type: Exact, Inexact) \times 5 (Inter-Stimulus Interval: 0, 20, 40, 449 80, 160 ms) within-subjects design was used. The new variable in this experiment was 450 Color Type. For those trials in which there was a match between the memory color and 451 one or more of the Ternus elements, half of the time it was an exact match and the other 452 have it was inexact (i.e., a different exemplar from the same color category). The factor 453 ISI was reduced by one level in order to decrease the number of conditions. All factors 454 were completely counterbalanced and randomly mixed within blocks of trials for a total 455 of 8 repetitions of the full design.

456 Data analysis: We again calculated the mean error rates in the memory task for each 457 participant and replaced participants that had an error rate higher than 25%, which 458 resulted in the replacement of one participant. The mean error rate of the remaining 459 participants was 13.88%. We also replaced a participant that showed a strong ISI effect 460 in all no-bias conditions that was in the opposite direction of that shown by all the other 461 participants, and that we therefore believe accidentally inverted the response keys. 462 Finally, trials with key presses other than the response keys (0.23 %) and extreme long 463 RTs (> 8000 ms, 0.71 %) were also eliminated as in Experiment 1.

464 **Results and Discussion**

465 The results were very similar to those of Experiment 1. Mean Group Motion466 responses are shown for the competitive-bias and no-bias conditions separately in

467 Figure 5. We first conducted a 5 (Memory Color: EB-Match, GB-Match, Third-Match, 468 No-Bias Match, No-Bias No-Match) × 2 (Color Type: Exact, Inexact) × 5 (Inter-469 Stimulus Interval: 0, 20, 40, 80, 160 ms) repeated measures ANOVA on individual 470 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, 471 $F(16,176) = 4.55, p < .001, adj.\eta_p^2 = .23$, (no Greenhouse-Geisser correction possible), 472 but no other significant interactions with Memory Color, Fs < 1.66, p > .177, $adj.\eta_p^2 <$ 473 474 .05. Holms corrected paired t-tests revealed that all levels of the factor Memory Color 475 differed significantly from each other, t(11) > 2.83, $p_{holm} < .49$, $adj.\eta_p^2 = .37$, with the 476 exception of the comparison between 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 477 478 condition, t(11) = 1.01, $p_{holm} = .636$, $adj.\eta_p^2 = .002$.

479 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 480 481 responses in the competitive-bias display (Figure 5, left) were submitted to a 3 (Memory 482 Color: EB-Match, GB-Match, Third-Match) × 2 (Color Type: Exact, Inexact) × 5 (Inter-483 Stimulus Interval: 0, 20, 40, 80, 160 ms) repeated measures ANOVA. There was a 484 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, $adj.\eta_p^2 =$ 485 486 .28. In addition, there was 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, 487 $F(2,22) = 2.66, p = .092, adj.\eta_p^2 = .12$. None of the other interactions were significant, 488 $F_{\rm s} < 1.10, p > .370, adj.\eta_p^2 < .008$. Follow up comparisons confirmed that, as in 489 490 Experiment 1, group motion responses were higher for the GB-Match condition (49%)

than for the EB-Match condition (33%), t(11) = 3.09, $p_{\text{holm}} = .021$, $adj.\eta_p^2 = .42$. They 491 492 were also higher for the GB-Match condition (49%) than the Third-Match condition 493 (30%), t(11) = 3.91, $p_{\text{holm}} = .007$, $adj.\eta_p^2 = .54$. There was no reliable difference 494 between the EB-Match and the Third-Match condition t(11) = 1.01, $p_{\text{holm}} = .334$, $adj.\eta_p^2$ 495 = .002. Given the trend of an interaction between Memory Color and Color Type, we 496 conducted separate post-hoc ANOVAs for each Color Type condition. The main effect 497 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 =498 .001, $adj.\eta_p^2 = .43$. The pattern of effects for exact color matches was the same as in the 499 500 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 501 502 responses in the GB-Match condition (51 %) than in the Third-Match condition (31 %), t(11) = 3.31, $p_{\text{holm}} = .021$, $adj.\eta_p^2 = .45$, but no significant difference between the EB-503 504 Match and the Third-Match conditions, t(11) = -0.19, $p_{\text{holm}} = .850$, $adj.\eta_p^2 = -.09$. For 505 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, $p_{holm} =$ 506 507 .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, $p_{\text{holm}} = .060$, $adj.\eta_p^2 = .30$, and EB-508 Match (36 %) versus Third-Match (29 %), t(11) = 2.18, $p_{\text{holm}} = .060$, $adj.\eta_p^2 = .24$. 509 510 Overall then, the exact match conditions of Experiment 2 replicated the pattern of data 511 observed in Experiment 1, and the inexact match condition yielded a weaker version of 512 this pattern. 513 Next, mean group-motion responses in the no-bias display condition (Figure 5

514 right) were submitted to a 3 (Color Match: Exact-Match, Inexact-Match, No-Match) × 5

- 515 (Inter-Stimulus Interval: 0, 20, 40, 80, 160 ms) repeated measures ANOVA. There was
- 516 a main effect of ISI, F(4,44) = 10.61, p = .002, $adj.\eta_p^2 = .44$, with group motion
- 517 responses ranging from 49 % for the 0 ms ISI to 86 % for the 160 ms ISI. There was no
- 518 significant effect of Color Match, F(2,22) = 0.29, p = .749, $adj.\eta_p^2 = -.063$, and no
- 519 interaction between the two factors, F(8,88) = 0.75, p = .645, $adj.\eta_p^2 = -.021$.



Figure 5. Experiment 2: The left graph shows mean percent of group motion responses
as a function of ISI, Memory Color and Color Type in the competitive-bias display
conditions. The right graph represents mean percent of group motion responses as a
function of ISI and Color Match in the no-bias display condition. Standard errors
represent within-subject SEs after Cousineau-Morey (Cousineau, 2005; Morey, 2008).



533 condition 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 534 535 and Color Type in the competitive display was not significant, it is reminiscent of a 536 recent study showing that the motion history of elements in Ternus displays can bias 537 correspondence, but only if the type of historical motion (i.e., smooth versus apparent) 538 matches that of the Ternus display (Stepper, Moore et al., 2020). This suggests that the 539 representations of the objects held in memory need to match the visible stimuli very 540 closely in order to have an effect on correspondence. That is, the comparison operation 541 appears to be quite specific. Future research can systematically manipulate the 542 magnitude of feature differences to more precisely characterize the relationship between 543 correspondence and feature similarity.

544

Experiment 3: Size memory task with color being incidental

545 In Experiment 3 we examined the generality of the effect of VWM content on 546 correspondence processes. In particular, we asked whether VWM content that is 547 incidental to the explicit memory task can also impact correspondence, or alternatively, 548 if it is only the information that is being held active in the service of the current task that 549 influences correspondence. The memory task was changed to report the size of a 550 rectangle rather than its color (see Hollingworth & Luck, 2009). It happened to be a 551 particular color, that did or did not match some of the elements of the Ternus displays, 552 but participants were not asked to remember the color and were not tested on it. The 553 question was whether the color, incidentally encoded along with the size of the 554 rectangle, would bias Ternus motion. If it did, then it would confirm that even

555 incidentally encoded content is factored into the correspondence process. By way of 556 preview, incidental color did not bias the perception of Ternus motion.

557 Methods

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.

561 Stimuli. The Ternus display was exactly the same as in Experiment 1. For the memory 562 task, the to-be-remembered stimulus was a rectangle that varied in size from 1.76° and 563 2.91° (randomly selected). The color of the rectangle was one of the four colors used in 564 Experiment 1, and color-match to the Ternus display was defined in the same way as in 565 Experiment 1. At the end of the trial, two squares were presented, one that was the 566 same size as the original to-be-remembered square (target) and one that was 0.62° 567 smaller or 0.62° larger than the target square (foil). Both squares were the same color as 568 the original square. The sides of the target and foil were selected randomly on each 569 trial.

570 *Task.* The Ternus task was exactly the same as in Experiments 1 and 2. For the memory 571 task, participants indicated which of two rectangles, the left or the right, matched the 572 size of the rectangle presented at the beginning of the trial.

573 *Procedure and Design.* The procedure and design were the same as in Experiment 1.

574 *Data analysis:* As in the previous two experiments we calculated the mean error rates in 575 the memory task for each participant and replaced participants with error rates higher

- 577 14.12 %. Trials with key presses other than the response keys (0.13 %) and extreme
- 578 long RTs (> 8000 ms, 0.15 %) were also eliminated, as in the previous experiments.

Mean Group Motion responses are shown for competitive-bias and no-bias

579

580

Results and Discussion

581 displays separately in Figure 6. We first conducted a 2 (Display: competitive-bias, no-582 bias) × 4 (Memory Color: EB-Match, GB-Match, Third-Match, No-Match) × 6 (ISI: 0, 583 20, 40, 80, 160, 300 ms) repeated measures ANOVA on individual mean group motion 584 responses. In contrast to Experiment 1, there was no main effect of Display, F(1,11) =585 1.24, p = .289, $adj.\eta_p^2 = .02$, no interaction between Display and Memory Color, F(3,33) = 1.29, p = .294, $adj_{1}n_{p}^{2} = .02$, and no three-way interaction between all three 586 factors, F(15,165) = 0.93, p = .534, $adj_{.}\eta_{p}^{2} = -.006$. There was, however, an interaction 587 between Display and ISI, F(5,55) = 11.80, p < .001, $adj.\eta_p^2 = .47$. 588 589 To allow for comparison with Experiment 1 and to investigate the effect of 590 working memory content, we conducted separate analyses for the two display

591 conditions. Individual mean group responses for the competitive-bias display (Figure 6,

592 left) were submitted to a 4 (Memory Color: EB-Match, GB-Match, Third-Match, No-

593 Match) \times 6 (ISI: 0, 20, 40, 80, 160, 300 ms) repeated measures ANOVA. There was a

594 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,
- 596 however, no effect of Memory Color, F(3,33) = 2.51, p = .130, $adj.\eta_p^2 = .11$, and no
- 597 interaction between Memory Color and ISI, F(15,165) = 1.01, p = .452, $adj.\eta_p^2 =$
- 598 .0008.





610 Figure 6. Experiment 3: Mean percent of group motion responses as a function of ISI 611 and the Memory Color. The left graph shows the competitive-bias display condition for each of the four memory color match conditions, element bias match (EB-Match), group 612 613 bias match (GB-Match), third element color match (Third-Match) or no element color 614 match (No-Match). The right graph represents the no-bias display condition, the 615 Memory Color either matching the element's color (Match) or not (No-Match). Standard 616 errors represent within-subject SEs after Cousineau-Morey (Cousineau, 2005; Morey, 617 2008).

618 In summary, unlike in Experiments 1 and 2, colors held in VWM did not bias 619 correspondence in Ternus displays. The difference between this experiment and the 620 previous two is that participants were not required to explicitly encode color. Assuming 621 that color was incidentally encoded when memorizing the size of the to-be-remembered 622 square, then, there is no evidence that this incidental memory content interacts with the 623 correspondence process. We do not have a separate measure of whether or not color 624 was encoded, and so we cannot rule out the possibility that it was not. However, 625 previous studies using this general strategy in the context of asking whether incidentally 626 encoded color information can interact with attentional guidance, found that it did 627 (Hollingworth & Bahle, 2020; Hollingworth & Luck, 2009; Hollingworth et al., 2013a, 628 2013b; but see Olivers et al., 2006). Participants in the study by Hollingworth and Bahle 629 (2020), for example, had to remember the size of a colored item, exactly as in our study. 630 They then had to search an array for an object with a certain target feature (the 631 orientation of a "c"). The color of the object could match that of the item memorized or 632 not. Participants were faster to detect the target on the object when its color matched the 633 memory color than when it did not, despite the memory color being incidental and 634 completely irrelevant to the task. Similar effects of incidental memory features 635 influencing visual search have been shown for different types of search tasks, different 636 dependent measures, and different memory and stimulus feature dimensions (Bahle et 637 al., 2018; Foerster, & Schneider, 2018; Hollingworth & Luck, 2009; Hollingworth & 638 Matsukura, 2019; Hollingworth et al., 2013a, 2013b). We have little reason to suspect, 639 therefore, that color was not similarly incidentally encoded in this experiment. Note also 640 that biasing effects from incidental features in VWM have been most consistently

observed in paradigms probing oculomotor orienting, a measure that is particularly

642 sensitive to VWM-based guidance (Bahle et al., 2018).

643

General Discussion

644 This study investigated the influence of VWM content on correspondence 645 processes using Ternus motion. Prior to viewing competitive-bias Ternus displays 646 (Figure 1C), observers were shown a color to commit to memory for later report. When 647 the memory color matched the element-bias color, more element motion was reported, 648 whereas when the memory color matched the group-bias color, more group motion was 649 reported (Experiments 1 and 2). These results confirm that VWM content can 650 contribute to correspondence as expected given the assertion that the function of 651 correspondence is to support continuous representations of objects in the world even 652 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 653 654 information was maintained in VWM, this result indicates a limitation of the impact of 655 VWM content on correspondence processes that further studies could confirm and 656 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 664 competition for awareness in binocular rivalry (e.g., Alpers & Pauli, 2006; Anderson et 665 al., 2011; Paffen et al., 2011; Sheth & Pham, 2008), as can VWM content (Scocchia et 666 al., 2014) and attention (e.g., see Dieter, & Tadin, 2011; Paffen & Alais, 2011 for 667 reviews). And finally, most directly comparable to the current work, are demonstrations 668 of memory content influencing perceptual ambiguities in dynamic displays, including 669 VWM content biasing perceptions of bistable shape-from-motion displays (Scocchia et 670 al., 2013) and long-term semantic memory content influencing apparent motion (Chen 671 & Zhou, 2011; Hsu et al., 2015; Ramachandran et al., 1998; Tse & Cavanagh, 2000; Yu, 672 2000). The current work brings together many of the design features of those previous 673 studies and adds to them by providing insight into higher-level influence on object 674 correspondence processes, in particular, as the ambiguity in Ternus motion, unlike the 675 ambiguity in, for example, binocular rivalry and figure-ground perception seems to 676 concerns correspondence processes at higher level of processing (Hein & Moore, 2014; 677 Stepper et al., in press; see also Moore et al., 2020, for the distinction between motion 678 and object correspondence).

679 One important question regarding perceptual biasing effects of the sort reported 680 here and those just reviewed is to what extent, if any, are they mediated by the orienting 681 of attention to a specific Ternus element? Any given bias effect might reflect a direct 682 influence of the biasing factor on the process in question. In the case of the current 683 study, for example, that would be a direct effect of activating a feature in visual working 684 memory enhancing the perception of one set of elements over another, thereby 685 influencing correspondence. Alternatively, a given bias effect might reflect an indirect 686 effect via attentional orientation. In the case of the current study, for example, it is 687 possible that holding a given feature in VWM caused attention to be guided to the

688 Ternus element of that color, as it is known to do (Olivers et al., 2006; Soto et al., 689 2005), which in turn might have biased correspondence in the Ternus display, as it is 690 also known to do (Stepper, Rolke et al., 2020). The current study cannot discriminate 691 between these alternatives. It is important to note, however, that if the impact of VWM 692 content on the perception of Ternus motion is mediated by attention, it is not due to a 693 strategic allocation of attention that is peculiar to the details of the current experiments. 694 That possibility was ruled out in Experiment 2. Rather, it would reflect an important 695 mediating relationship between attention and correspondence processes, a relationship 696 that is an important question for further research.

In summary, the current study builds on earlier work testing the range of factors 697 698 that determine object correspondence. In addition to spatiotemporal coherence and 699 feature similarity—both image level and perceived—between stimuli, we have 700 confirmed that VWM content contributes to correspondence processes. This is a 701 significant addition to our understanding, because the feature information that is held in 702 VWM is only mentally represented and not directly available in the image at the time 703 that correspondence is established. It is, therefore, the kind of information that a system 704 whose function it is to maintain the continuity of object representations across time and 705 space would need to rely on (e.g., Hollingworth et al., 2008). There remain open 706 questions regarding exactly what aspects of VWM content can influence 707 correspondence. We found that incidentally encoded information did not, but there is 708 much to be explored in this regard. We also do not know exactly what role attention 709 plays in this process. We do know, however, that correspondence can be resolved on 710 the basis of information that exists only in the viewer's memory and that it does so even 711 when that information is irrelevant to that task.

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