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When a static stimulus appears successively at two distant locations, we perceive illusory motion of the stimulus across them–long-range apparent motion (AM). Previous studies have shown that when the apparent motion stimuli differ in shape, interpolation between the two shapes is perceived across the AM path. In contrast, the perceived color during AM has been shown to abruptly change from the color of the first stimulus into that of the second, suggesting interpolation does not occur for color during AM. Here, we report the first evidence to our knowledge, that an interpolated color, distinct from the colors of either apparent motion stimulus, is represented as the intermediate percept on the path of apparent motion. Using carefully chosen target colors—cyan, pink, and lime—that are perceptually and neurally intermediate between blue and green, orange and magenta, and green and orange respectively, we show that detection of a target presented on the apparent motion path was impaired when the color of the target was "in-between" the initial and terminal stimulus colors. Furthermore, we show that this feature-specific masking effect for the intermediate color cannot be accounted for by color similarity between the intermediate color and the color of the terminal inducer. Our findings demonstrate that intermediate colors can be interpolated over the apparent motion trajectory as in the case of shape, possibly involving similar interpolation processes for shape and color during apparent motion.

Introduction

When a static stimulus appears successively at two different locations, we perceive motion of the stimulus across the two locations; this is known as long-range apparent motion (AM; Kolers, 1972; Korte, 1915; Wertheimer, 1912). Moreover, when the spatiotemporal parameters of the stimulus are optimal, the percept has not only a sense of illusory motion but also consists of a smooth transition of a well-defined object from one location to another, though no physical inputs are actually present along the path (Wertheimer, 1912).

Previous studies demonstrate that these illusory representations generated along the apparent motion path can interact with physically-presented stimuli (Hogendoorn, Carlson, & Verstraten, 2008; Yantis & Nakama, 1998). Yantis and Nakama (1998) showed that detection of targets is impaired when they are presented on the apparent motion path, suggesting that bottom-up stimuli can be masked by an illusory "token" created by apparent motion (apparent-motion-induced masking effect). Moreover, Schwiedrzik, Alink, Kohler, Singer, and Muckli (2007) found that this interaction is strongest when the target is presented spatiotemporally in time with the presumed intermediate apparent motion representation.

More recent studies suggest that this illusory token is not only spatiotemporal but also incorporates visual features of the apparent motion stimuli (Hidaka, Nagai, Sekuler, Bennett, & Gyoba, 2011). For example, using oriented Gabors, Hidaka et al. (2011) demonstrated that target orientations, similar to the orientation of the apparent motion inducers, were more difficult to detect on the apparent motion path. Furthermore, when the inducers changed their orientation during apparent motion, causing a percept of a rotation, detection of targets with orientations similar to the presumed intermediate was impaired. This suggests that intermediate visual features of two different AM inducers are interpolated during apparent motion.

Conversely, unlike orientation, studies with stimuli changing color in apparent motion failed to show an

interpolation along the apparent motion path. Kolers and von Grünau (1976) found that when observers viewed apparent motion between red and green or blue and yellow stimuli, the perceived color along the apparent motion path appeared to abruptly change from the color of the first stimulus into that of the second, without any percept of an intermediate color on the path. Souto and Johnston (2012) also showed that the apparent color of a probe on the apparent motion path is biased toward the color of the AM-inducing stimuli, indicating the absence of feature interpolation for color. Based on these findings, it was proposed that transitions of form and color occur in different manners, the former being continuous and the latter being discrete (Kolers & von Grünau, 1976).

However, due to several limitations of previous studies, it still remains inconclusive whether intermediate colors can be represented along the AM path. For example, Kolers and von Grünau (1976) found that color experience was matched to the color of the initial AM inducer when the fixation point was close to the position of the initial inducing stimulus, whereas it was matched to the color of the terminal AM inducer when the fixation was close to the position of the terminal-inducing stimulus. Since a direct color-matching paradigm was used in Kolers and von Grünau (1976), this result can be due to a perceptual bias to either the initial or terminal color. Also, it may be difficult to compare the illusory percept during AM directly with physically present colors. On the other hand, Souto and Johnston (2012) instructed subjects to report the presence of targets on the AM path, regardless of their color, and measured how target detection threshold is affected by AM, overcoming the limitation of the color-matching paradigm. However, a possible intermediate color for their AM inducers (i.e., yellow for red/green) as well as other nonopponent inducer color pairs in Kolers and von Grünau (1976) were not tested.

Here, we examine whether another color, distinct from the colors of the initial and terminal AM stimuli, can be interpolated as the intermediate percept on the path of AM while avoiding the limits of previous studies. We employed a target detection task measuring elevation of detection threshold induced by AM to avoid a possible response bias, and explicitly tested intermediate colors that are distinct from the color of inducers to probe feature interpolation along the AM path. The chromaticities of initial, terminal, and intermediate colors were chosen based on chromatic contrast, so that the possible intermediate color was neurally, as well as perceptually, intermediate between two AM-inducing colors. For example, with a blue/green pair, we set cyan as an intermediate color. The color, cyan, is intermediate in terms of a neural mechanism (blue induces high S-cone excitation, green induces low S-cone excitation, and cyan induces middle

level S-cone excitation with fixed L-cone excitation level; see Figure 2B) as well as in terms of its percept based on color mixture (cyan is also called "blue-green," which is an additive mixture of blue and green). We also tested two other pairs of colors (orange/magenta and green/orange) to confirm that representation of intermediate colors along AM-path is not specific to a particular color pair.

In Experiment 1, using a blue/green pair, we first test if an AM-induced masking effect is found when the color of a target presented on the AM path matches the intermediate color, cyan. In Experiment 2, we rule out the account that the results in Experiment 1 are due to color similarity between the intermediate color (cyan) and the color of terminal inducers (green). Other color pairs, orange/magenta and green/orange are tested in Experiments 3 and 4 in order to examine the generalizability of intermediate color interpolation during AM. In Experiment 5, we replicate findings in previous studies using an opponent color pair (red/green). Our findings suggest that, as in the case of orientation, a color that is not presented elsewhere in the retinal input, but that is interpolated between the apparent motion stimuli, can be represented during dynamic transitions over the apparent motion trajectory.

Methods

Observers

Sixteen observers participated in Experiment 1; 15 observers participated in Experiment 2, six of whom also took part in Experiment 1; 16 observers participated in Experiment 3, five of whom also participated in Experiment 1; 12 observers participated in Experiment 4, five of whom also participated in Experiment 1; and 10 observers participated in Experiment 5, two of whom also participated in Experiment 1. All observers had normal or corrected-to-normal visual acuity and normal color vision. All observers were financially compensated for their time and gave informed written consent within a protocol approved by the Committee for the Protection of Human Subjects at Dartmouth College. All observers were naïve to the purpose of the study.

Stimuli and procedure

The observers were tested in a dimly lit room at a viewing distance of 57 cm from a 17-inch Mitsubishi CRT monitor (1024 × 768 pixels, 75 Hz; Mitsubishi, Tokyo, Japan) whose R, G, B guns were calibrated using a spectroradiometer (Ocean Optics USB4000, Dunedin, FL) and a luminance meter (Minolta LS100, Ramsey, NJ), creating a color look-up-table (8-bit for
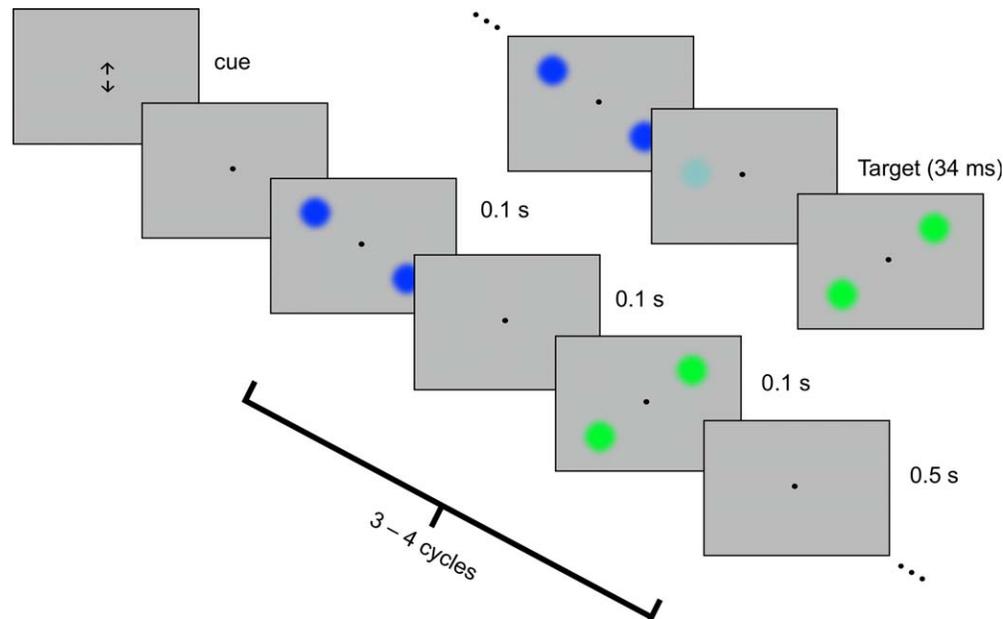
Figure 1. Stimulus presentation order shown to observers in Experiment 1.

R, G, and B). Head and chin rests were used to stabilize their heads for the duration of the study. Stimuli were created and displayed with MATLAB using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). We utilized a modified version of the "bistable quartet" (Ramachandran & Anstis, 1983; Ternus, 1938), in which two colored Gaussian blobs (1.8° in radius, $\sigma = 0.2$, 5.7° to 9° in eccentricity) at diagonally opposite corners of an imaginary square are alternately presented with two blobs at the other opposite corners (Figure 1). The resulting percept is bistable, in that either a horizontal or a vertical direction of apparent motion is possible to perceive at any given moment. Observers maintained their fixation at a point in the center of the imaginary square while perceiving the AM stimuli. They first practiced switching their percept between horizontal and vertical apparent motion until they could do so for three consecutive trials. Also, the horizontal and vertical distance between the centers of the blobs was adjusted for each observer so that they could perceive either direction with ease (average horizontal distance across observers: 3.5° to 6°; vertical distance: 4° to 6.5°). At the beginning of each block, observers were cued with an arrow to see either vertical AM (On-path) or horizontal AM (Off-path) and pressed the space-key to start the block of 20 trials. On each trial, five cycles of apparent motion were presented with 500 ms intercycle interval. Stimulus duration and interstimulus interval (ISI) were both 100 ms.

A two-alternative forced choice (2AFC) task was used to measure the chromaticity contrast threshold for the detection of a target during apparent motion. A target patch, the same Gaussian blob as the apparent

motion inducers but low-contrast, was presented for 34 ms (ISI: 33 ms) at the midpoints of either the left or right of the two vertical apparent motion paths on the third or fourth motion cycle. They were on the apparent motion path (On-path) when vertical AM was perceived but were no longer on the path (Off-path) when horizontal AM was seen. Observers reported on which apparent motion path the target appeared by pressing the "Z" (left) or "M" (right) keys. If on a given trial observers perceived the incorrect direction of motion, they were asked to press the "V" key, and those trials were excluded from data analysis (an average of 2.6% (Experiment 1), 1.7% (Experiment 2), 3.6% (Experiment 3), 1.1% (Experiment 4), and 0.8% (Experiment 5) of trials per observer). The next trial commenced after observers made their response. The bistable quartet stimulus guarantees that any effect between the on-path and off-path conditions is not due to physical differences in the stimulus.

In Experiment 1, the colors of the initial and the terminal inducers were blue ($l = 0.627$, $s = 5.0$) and green ($l = 0.627$, $s = 0.2$) respectively, which vary only in their S-cone excitation level with fixed L-cone excitation level. At its highest saturation, the target was one of four colors (Figure 2A): matching either the color of the initial inducers (blue), the color of the terminal inducers (green), the presumed in-between color between the two inducer colors (cyan: $l = 0.627$, $s = 1.0$), or a control color at the same S-cone excitation level as the in-between color, cyan, but in the opposite polarity in L-cone excitation (pink: $l = 0.707$, $s = 1.0$). The control color was included to allow for a comparison baseline detection threshold. The chromaticity values of the targets and inducers are shown on the modified
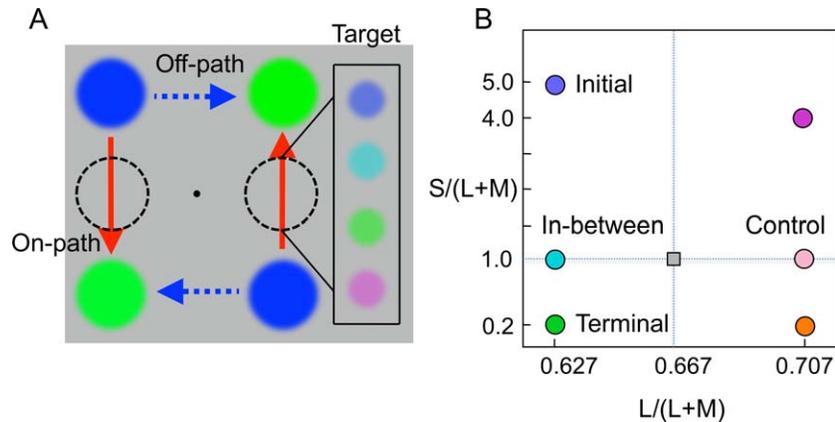
Figure 2. (A) Stimuli and target conditions in Experiment 1. (B) Four target colors (Blue: initial, Cyan: intermediate, Green: terminal, and Pink: control) used in Experiment 1 and two other colors (orange and magenta) used in Experiment 2 displayed in Cone-Excitation Chromaticity space (MacLeod & Boynton, 1979).

Cone-Excitation color space (MacLeod & Boynton, 1979), which is based on Smith and Pokorny (1975) cone fundamentals, in Figure 2B. To measure the sensitivity of detecting each perceived color on the apparent motion path while excluding the influence of luminance contrast, the colors of the stimuli were individually set at each observer's equiluminant level at 10 cd/m^2 using a minimum motion technique (Anstis & Cavanagh, 1983). The stimuli were presented on an equal-energy-spectrum (EES) "white" background that was also equiluminant to the target (10 cd/m^2). For each target color, we measured the chromatic contrast threshold for detecting a target at 80% accuracy using QUEST (Watson & Pelli, 1983). Within each QUEST procedure, chromatic contrast of the target was manipulated by adjusting both L- and S-cone contrast when the target color was either the initial or terminal color. When the target color was either the intermediate or control color, L-cone contrast was adjusted in Experiment 1, 2, and 3, and S-cone contrast was adjusted in Experiment 4. The chromatic contrast was adjusted in terms of "percent of maximum contrast" for each target color. There were 16 blocks of 320 trials in total, eight horizontal AM and eight vertical AM, consisting of 20 trials each. The order of the blocks was randomized for each observer. The side on which a target appeared (left vs. right) and the color of a target were randomized within a block. The contrast threshold for each condition (target color [4] × apparent motion [2]) was estimated based on 40 trials.

Experiment 1

In Experiment 1, we examine whether an intermediate color that is distinct from the inducers' colors can be interpolated on the apparent motion path. More

specifically, using a blue/green pair, we test if color detection thresholds for a target presented on the apparent motion path increases (AM masking effect) when its color matches the intermediate color, cyan. If the intermediate color is represented along the AM path, we would expect to see a decrease in the target detection performance when the target patch's color is identical to the presumed intermediate color.

Results

A two-way repeated-measures analysis of variance (ANOVA) with a Greenhouse-Geisser correction (apparent motion [On-path and Off-path] × target color [blue, green, cyan, and pink]) on target detection thresholds revealed a significant effect of apparent motion, $F(1, 15) = 4.683$, $p = 0.047$, consistent with the apparent motion masking effect reported in previous studies (Hidaka et al., 2011; Hogendoorn et al., 2008; Yantis & Nakama, 1998). A main effect of target color was also significant, $F(1.688, 25.323) = 17.961$, $p < 0.001$, mainly due to the lower threshold for blue targets compared to other colored targets (Blue: $M = 10.907$, $SE = 2.607$; Cyan: $M = 29.239$, $SE = 4.424$; Green: $M = 18.663$, $SE = 2.325$; Pink: $M = 18.486$, $SE = 1.961$). Crucially, an interaction between AM and target color was significant, $F(1.668, 25.018) = 4.679$, $p = 0.024$, indicating that apparent motion-induced masking is modulated by the color of the target (Figure 3).

To further compare the size of the apparent motion-induced masking effect across the four target colors and to remove individual biases, we calculated the AM masking index, a normalized difference score between On- and Off-path thresholds for each color as (On-path-Off-path)/AVE(On-path+Off-path). A high AM masking index would reflect an asymmetry in the target detection threshold for on-path versus off-path appar-
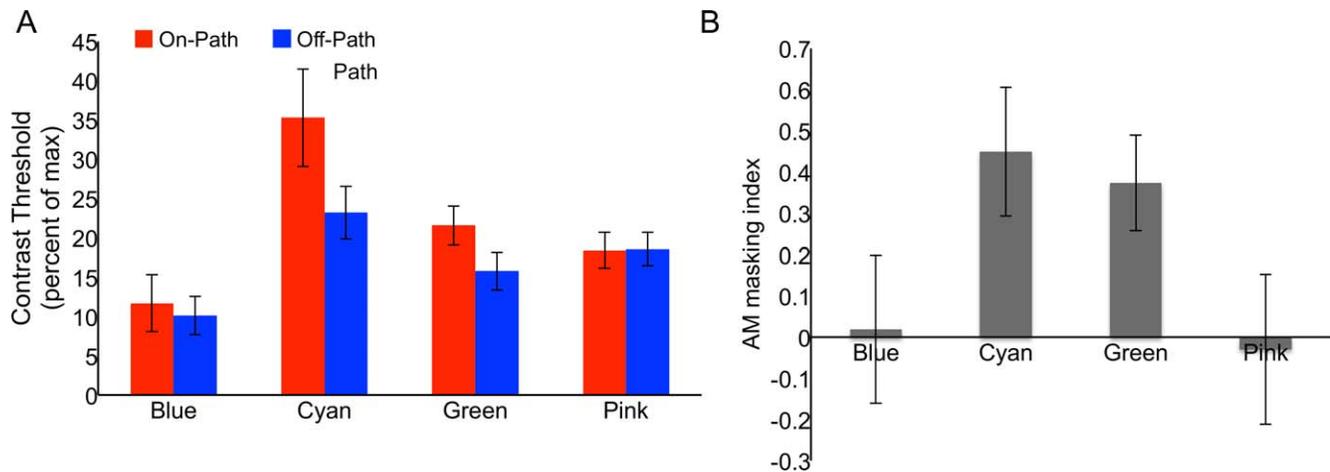
Figure 3. (A) Average color contrast thresholds (percent of max) for target detection in the On-path and Off-path conditions for each target color in Experiment 1. (B) AM masking effect for each target color. Error bars in this figure and subsequent ones show ±1 SE of the mean.

ent motion, and would manifest only if AM masking is indeed present. An ANOVA comparing the AM masking index for each target color confirmed a significant effect of color, $F(3, 45) = 3.158$, $p = 0.034$. Subsequent paired t-tests revealed that the significant masking effect compared to the control color is shown for both cyan, the presumed intermediate color between the AM stimuli (Cyan: $M = 0.449$, $SEM = 0.157$; Pink: $M = -0.030$, $SEM = 0.182$) [$t(15) = 2.325$, $p = 0.035$] and green, the color of the terminal inducers (Green: $M = 0.374$, $SEM = 0.116$) [$t(15) = 2.541$, $p = 0.023$]. The AM masking effect for green targets (color of the terminal inducers) is consistent with the previous finding (Kolers & von Grünau, 1976), indicating predictive color updating, and it can account for the marginally significant result in a linear contrast of cyan and other colors. There was no significant difference between the AM masking index for the blue target color (color of the initial inducers) compared to the control color (Blue: $M = 0.019$, $SEM = 0.180$) [$t(15) = 0.248$, $p = 0.807$].

These results indicate that an intermediate color between the colors of the apparent motion inducers can be interpolated on the AM path when the object's color transforms from one to another across the AM path. This representation of intermediate features in apparent motion is consistent with the previous finding in the case of apparently rotating oriented Gabors (Hidaka et al., 2011) suggesting the involvement of similar interpolation processes for shape and color over the course of apparent motion.

Experiment 2

We found impaired target detection for the in-between (cyan) and terminal (green) colors compared

to the control color (pink) when the target is presented on the apparent motion path in Experiment 1. The target detection impairment for the intermediate color suggests that interpolation of color can occur over the apparent motion trajectory. One alternative account is that only the terminal color (green) is represented on the AM path as previously found (Kolers & von Grünau, 1976), but because cyan is perceptually more similar to green (i.e., closer to green on CIE-Lab color space) than the other two colors, blue and pink, detection of cyan targets is also impaired. To rule this out, we conducted Experiment 2 using green for both the initial and terminal stimuli. If the color similarity between the intermediate and the terminal color contributed to the detection impairment for the intermediate color in Experiment 1, detecting cyan targets would still be impaired in this case.

Methods

The stimuli and procedures were the same as Experiment 1 except that both pairs of inducers were green ($l = 0.627$, $s = 0.2$).

Results

A repeated-measures ANOVA with a Greenhouse-Geisser correction revealed a significant main effect of apparent motion, $F(1, 14) = 7.792$, $p = 0.014$, and target color (Blue: $M = 6.585$, $SE = 0.850$; Cyan: $M = 19.375$, $SE = 2.490$; Green: $M = 28.205$, $SE = 6.123$; Pink: $M = 19.734$, $SE = 2.669$); $F(1.403, 19.642) = 10.545$, $p = 0.002$. As in Experiment 1, an interaction of apparent
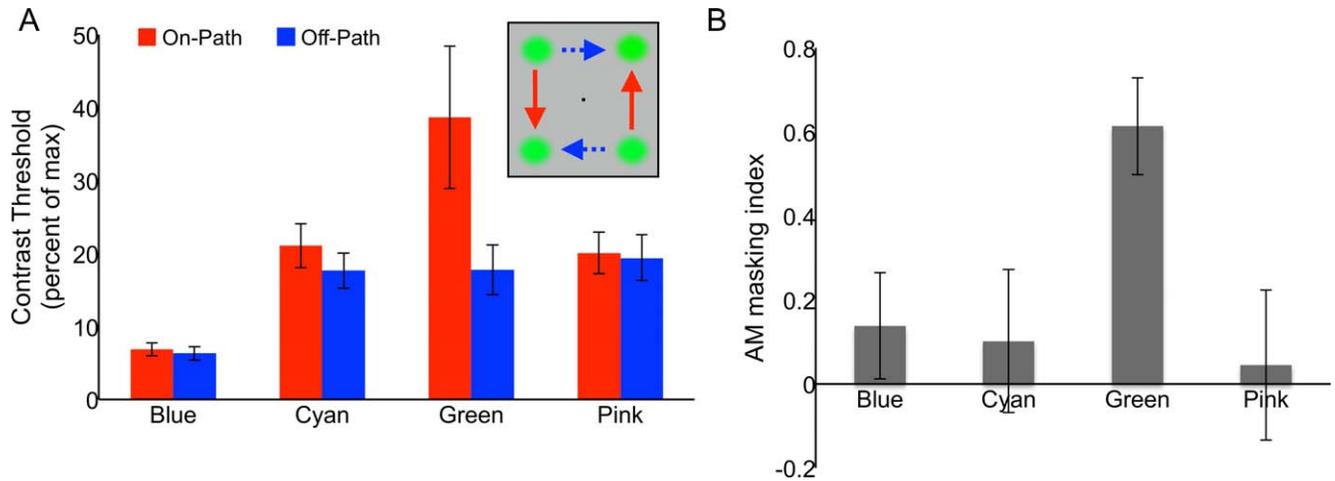
Figure 4. (A) Average color contrast thresholds for target detection in the On-path and Off-path conditions in Experiment 2. (B) AM masking effect for each target color.

motion and target color was also significant, $F(1.319, 18.462) = 5.348$, $p = 0.025$ (Figure 4).

A subsequent ANOVA comparing the AM masking index for each target color revealed a significant effect of color, $F(3, 42) = 2.906$, $p = 0.046$. Paired t tests on the AM masking index confirmed the increase of the AM-induced masking effect for green targets compared to the control color (Green: $M = 0.613$, $SEM = 0.115$; Pink: $M = 0.045$, $SEM = 0.179$) [$t(14) = 2.761$, $p = 0.015$]. However, there was no significant difference between the control color and either of the other two target colors (Cyan: $M = 0.102$, $SEM = 0.170$ [$t(14) = 0.266$, $p = 0.794$]; Blue: $M = 0.138$, $SEM = 0.126$ [$t(14) = 0.421$, $p = 0.680$]), indicating that a significant AM masking effect compared to a control color was found only for the inducers' color (green) but not for the color that is perceptually similar to the inducer color (cyan) when the color remains the same across the apparent motion path. These results are consistent with the previous findings (Kolers & von Grünau, 1976; Souto & Johnston, 2012) and suggest that the feature-specific masking effect for interpolated color found in Experiment 1 cannot be accounted for by color similarity between the interpolated color and the color of the terminal apparent motion stimulus.

Experiment 3

In order to show that the color updating during apparent motion observed in Experiment 1 is not specific to the color pair we chose (blue/green) but is a general phenomenon, we test another color pair (orange/magenta) that also varies only in the S-cone excitation level but has a different L-cone excitation level than the blue/green color pair. For this new color

pair, the intermediate color, pink, can be found by averaging the S-cone excitation values of the two inducers.

Methods

The stimuli and procedures were the same as Experiment 1 except for the colors of the inducers and the target. The colors of the initial and the terminal inducers were orange ($l = 0.707$, $s = 0.2$) and magenta ($l = 0.707$, $s = 4.0$), respectively, which like the blue/green pair only vary in S-cone excitation level but have the same L-cone excitation level (Figure 2B). At highest saturation, the color of the target was one of the following four: the initial inducers' color (orange), the terminal inducers' color (magenta), the intermediate color between the two inducers (pink: $l = 0.707$, $s = 1.0$), or a control color (cyan: $l = 0.627$, $s = 1.0$). Observers performed 48 practice trials at the start of the session and confirmed that they were able to switch between horizontal and vertical apparent motion with ease.

Results

A repeated-measures ANOVA revealed a significant effect of apparent motion, $F(1, 15) = 6.642$, $p = 0.021$, replicating an AM color masking effect for the new color pair. There was a main effect of target color, $F(3, 45) = 14.421$, $p < 0.001$, due to the lower threshold for magenta targets compared to other colored targets (Orange: 14.088, $SE = 1.832$; Pink: $M = 19.867$, $SE = 2.981$; Magenta: $M = 9.958$, $SE = 1.883$; Cyan: $M = 21.923$, $SE = 2.891$). However, an interaction between apparent motion and target color was not significant,
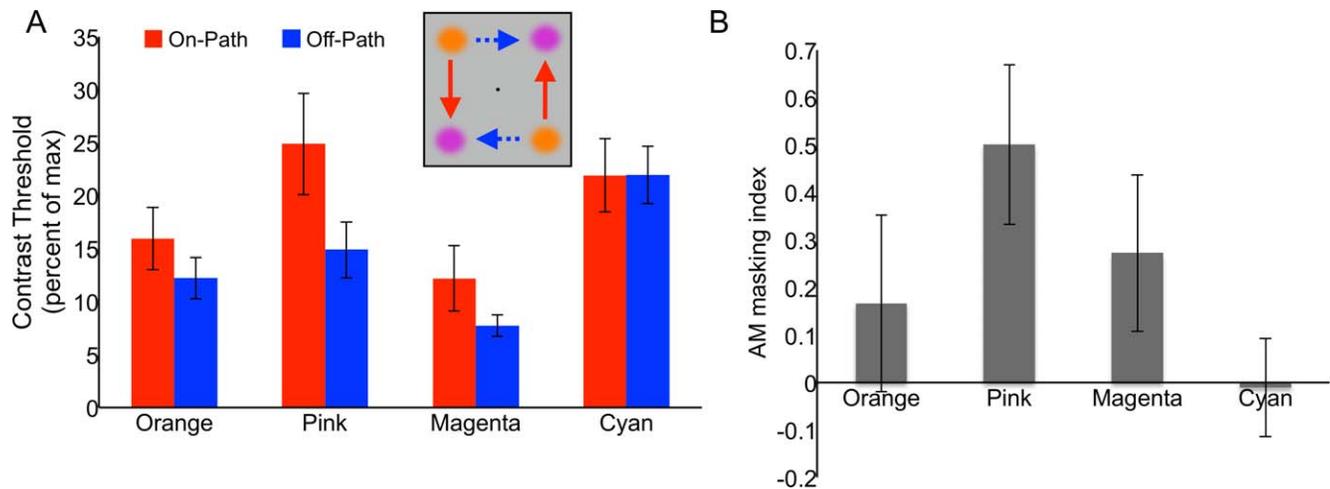
Figure 5. (A) Average color contrast thresholds for target detection in Experiment 3. (B) AM masking effect for each target color.

$F(3, 45) = 1.475$, $p = 0.234$ (Figure 5), unlike in Experiment 1 and 2.

An ANOVA comparing the AM masking index for each target color showed no effect of color, $F(3, 45) = 1.856$, $p = 0.151$. However, a subsequent paired t-test on the AM masking index revealed a significant masking effect for only the intermediate color, pink ($M = 0.501$, $SEM = 0.168$), compared to the control color (Cyan: $M = -0.010$, $SEM = 0.104$) [$t(15) = 2.543$, $p = 0.023$]. The AM masking index was not significantly different between the control color and the other two colors, orange and magenta (Magenta: $M = 0.273$, $SEM = 0.165$ [$t(14) = 1.341$, $p = 0.200$]; Orange: $M = 0.166$, $SEM = 0.185$ [$t(15) = 0.751$, $p = 0.464$]).

These results suggest that the color interpolation during AM is not specific to the color pair used in Experiment 1 (blue/green) but is also evident for other colors that vary only in their S-cone excitation levels.

Experiment 4

In the first set of three experiments, we used color pairs that differ only by their S-cone excitation levels, with fixed L-cone excitation levels. In order to examine whether target detection impairment is also evident for colors that vary only in their L-cone excitation levels (with fixed S-cone excitation levels), we essayed another color pair of green and orange inducers, which has an intermediate color of lime (yellowish green).

Methods

The stimuli and procedures were the same as Experiment 1 except for the colors of the inducers and targets. The colors of the initial and the terminal inducers were green ($l = 0.627$, $s = 0.2$) and orange ($l = 0.707$, $s = 0.2$), respectively (Figure 6A). At highest
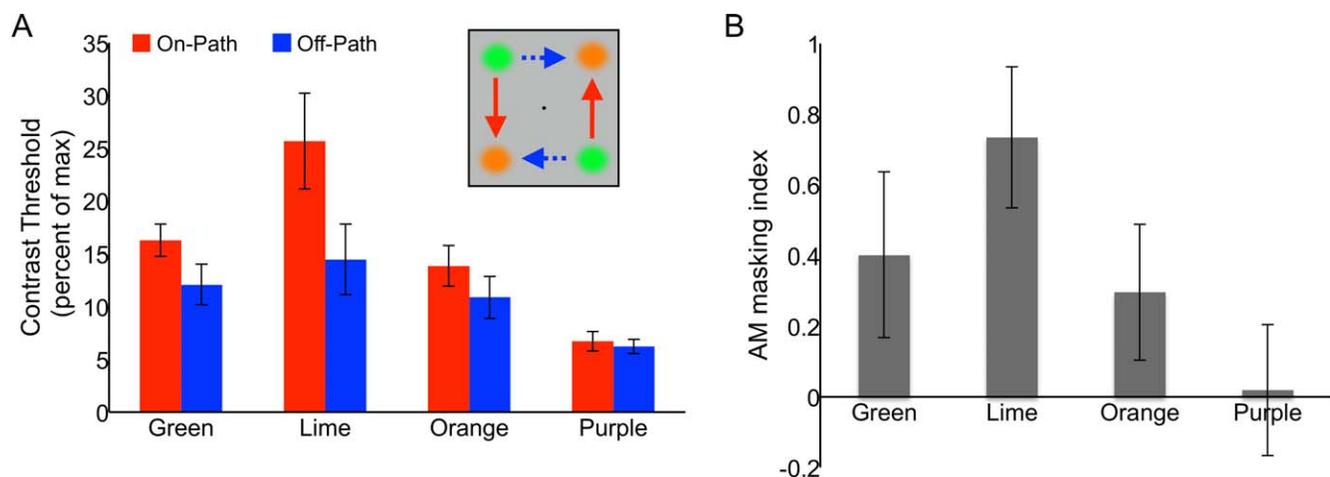

Figure 6. (A) Average color contrast thresholds for target detection in Experiment 4. (B) AM masking effect for each target color.
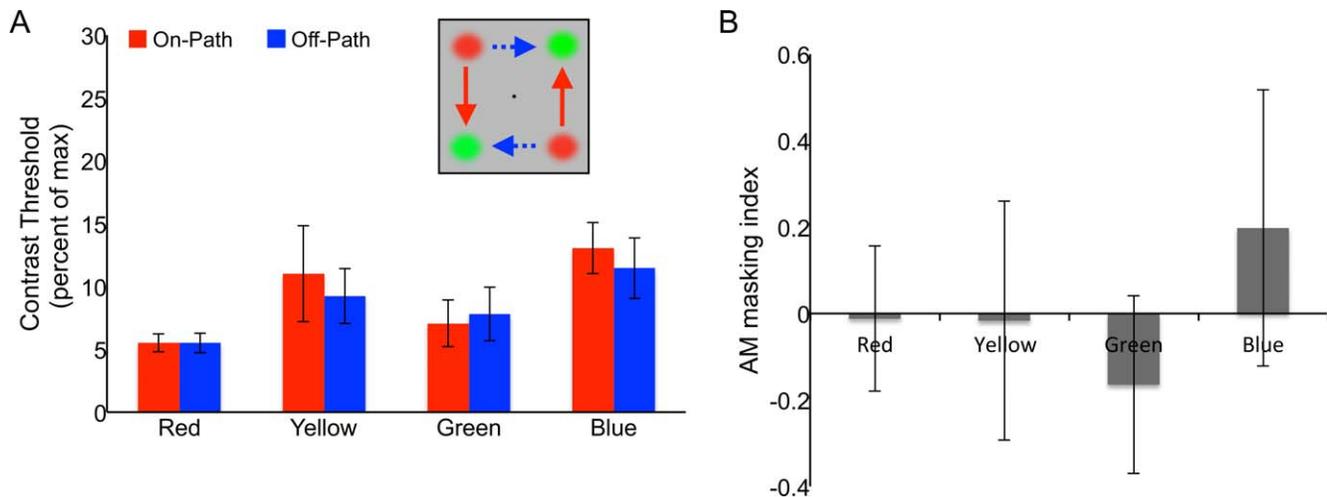
Figure 7. (A) Average color contrast thresholds for target detection in Experiment 5. (B) AM masking effect for each target color.

saturation, the color of the target was one of the following: the initial inducers' color (green), the terminal inducers' color (orange), the intermediate color between the two inducers (lime: $l = 0.667$, $s = 0.2$), or a control color with the same L-cone level as the intermediate color but opposite S-cone polarity (purple: $l = 0.667$, $s = 5.0$).

Results

A repeated-measures ANOVA showed significant effects of color, $F(1.596, 17.559) = 10.472$, $p = 0.002$; Greenhouse-Geisser corrected, and condition, $F(1, 11) = 9.689$, $p = 0.010$, as well as a significant interaction between condition and color, $F(3, 33) = 4.199$, $p = 0.013$. An ANOVA comparing the AM masking index for each target color showed a significant effect of color, $F(3, 33) = 3.296$, $p = 0.032$. Paired t-tests revealed a significant difference only between the intermediate color (Lime: $M = 0.734$, $SEM = 0.200$) and the control color (Purple: $M = 0.019$, $SEM = 0.186$) [$t(11) = 2.873$, $p = 0.015$], and no significant difference between the control color and either the color of the initial (Green: $M = 0.402$, $SEM = 0.235$) [$t(11) = 1.231$, $p = 0.244$] or terminal inducers (Orange: $M = 0.296$, $SEM = 0.186$) [$t(11) = 1.071$, $p = 0.307$].

These results suggest that the color updating during AM is not confined to color pairs that vary only in their S-cone excitation level, like those used in Experiments 1 (blue/green) and 3 (orange/magenta), but also occurs for color pairs that vary only in their L-cone excitation level (green/orange).

Experiment 5

Results from our four experiments suggest that the representation of color can be interpolated along the

apparent motion path when color transforms between a color pair that only varies along one dimension of chromatic channels (either S-cone or L-cone excitation level). These results are in contrast with the previous studies that found no evidence for color interpolation (Kolers & von Grünau, 1976; Souto & Johnston, 2012). One possible account for this discrepancy is that color interpolation may not occur under conditions where the color pairs vary along both chromatic channels. This possibility remains to be tested because when a color pair that varies in both chromatic channels was examined in the previous study using a masking paradigm similar to ours (Souto & Johnston, 2012), the masking effect of the intermediate color, based on an additive color mixture, was not explicitly tested. Here in Experiment 5, we aim to examine whether the AM masking effect can occur when the AM inducers' colors vary in both chromatic channels, using a red/green color pair that differs in both their L-cone and S-cone excitation levels and testing an intermediate color of yellow.

Methods

The stimuli and procedures were the same as Experiment 1 except for the colors of the inducers and targets. In this experiment we utilized the CIE color-space following Souto and Johnston (2012). The colors of the initial and the terminal inducers were red ($x = 0.617$, $y = 0.329$) and green ($x = 0.281$, $y = 0.600$), respectively (Figure 7A). At highest saturation, the target's color was one of the following: the initial inducers' color (red), the terminal inducers' color (green), the intermediate color between the two inducers (yellow), or a control color (blue: $x = 0.159$, $y = 0.090$). The chromaticity value for yellow was individually set for each observer using 6 calibration

trials. During a trial, subjects viewed a colored square (4.6 ° × 4.6 °) on either the left or right of central fixation (4° eccentricity) whose color ranged between a red-green ratio of 0.1–0.9. They were instructed to adjust the red-green ratio until the square appeared neither reddish nor greenish. Each observer completed three trials per side (left vs. right) and the final red-green ratio for each trial was averaged to compute their yellow value (range across subjects: $x = 0.421$–0.451, $y = 0.466$–0.491). The order of trials was randomized per subject and the red-green ratio at the beginning of each trial was randomized per trial.

Results

A repeated-measures ANOVA comparing AM and target color with a Greenhouse-Geisser correction revealed no significant effect of AM, $F(1, 9) = 0.349$, $p = 0.569$, or interaction between AM and color, $F(2.083, 18.751) = 0.265$, $p = 0.778$. An effect of color was significant, $F(1.693, 15.237) = 4.822$, $p = 0.028$ (Red: $M = 5.514$, $SE = 0.659$; Yellow: $M = 10.128$, $SE = 2.800$; Green: $M = 7.432$, $SE = 1.916$; Blue: $M = 12.266$, $SE = 1.363$).

An ANOVA comparing the AM masking index for each target color showed no significant effect of color, $F(3, 27) = 0.362$, $p = 0.781$, and subsequent paired t-tests also confirmed no significant difference between the AM masking index of the control color (Blue: $M = 0.198$, $SEM = 0.319$) and any other colors (Red: $M = -0.012$, $SEM = 0.168$ [$t(9) = -0.624$, $p = 0.548$]; Yellow: $M = -0.017$, $SEM = 0.319$ [$t(9) = -0.727$, $p = 0.486$]; Green: $M = -0.164$, $SEM = 0.205$ [$t(9) = 0.797$, $p = 0.446$]).

To directly test the hypothesis that color interpolation during AM would be specific to color pairs that vary only on one chromatic channel, we compared the AM-masking effect for intermediate color in this experiment with that of Experiments 1, 3, and 4 where AM inducer pairs change their colors along a single color axis only. We performed a two-way mixed ANOVA of target color (intermediate vs. control) and type of color axis manipulation (single: Experiments 1, 3, 4 vs. both: Experiment 5) on the AM-masking index. The main effect of target color was not significant, $F(1, 52) = 1.353$, $p = 0.25$], nor was the main effect of color axis manipulation, $F(1, 52) = 0.847$, $p = 0.362$. Crucially, the interaction between color and color axis manipulation was significant, $F(1, 52) = 6.906$, $p = 0.011$], indicating the AM-masking effect for intermediate color is modulated by color axis manipulation. When comparing Experiment 5 to each experiment separately, the interaction effect was significant for Experiment 3, $F(1, 24) = 4.433$, $p = 0.046$, and for Experiment 4, $F(1, 20) = 5.884$, $p = 0.025$, and it was marginally significant for Experiment 1, $F(1, 24) = 3.941$, $p = 0.059$. These results suggest that the color interpolation during AM is specific to color pairs that vary only on one chromatic channel, either S-cone or L-cone excitation level only, such as those used in Experiments 1 (blue/green), 3 (orange/magenta), and 4 (green/orange).

Discussion

Here we investigate how color is updated when it transforms during apparent motion. Unlike previous studies that showed no evidence of intermediate color representations on the apparent motion path (Kolers & von Grünau, 1976; Souto & Johnston, 2012), we found that the intermediate color, which is distinct from either color of the apparent motion inducers, can be interpolated during color transformation over the apparent motion paths. In contrast to the previous suggestion that form is updated continuously whereas color follows a discrete step from an initial to a terminal color in its transformation (Kolers & von Grünau, 1976), our finding suggests that color can also be interpolated during apparent motion, generating intermediate colors that are not present in the physical input, when it transforms to a new color during apparent motion.

The discrepancy between the previous studies and ours could be explained by the several key differences in the task and stimuli employed. First and most importantly, while early work (Kolers & von Grünau, 1976) and a more recent study (Souto & Johnston, 2012) used color pairs for which the intermediate colors can be ambiguous, we chose colors of the initial and terminal inducers and targets based on chromatic contrast varying in only one dimension of color space. More specifically, unlike the color pairs in previous work that differ both in their L-cone and S-cone excitation levels, the color pairs we used have either the same L-cone excitation level and differ only in their S-cone excitation level (blue/green and orange/magenta pair) or the same S-cone excitation level and differ only in their L-cone excitation level (green/orange pair). Thus, the intermediate color in our study can be defined by averaging cone excitation values of the inducers with a fixed cone excitation level in the other dimension. Interpolation of features during apparent motion may occur when it involves a simple form of updating along a single dimension of features (e.g., updating color only on one of the color axes). Consistently, when we tested a red/green pair that varies along both color axes, we did not observe a significant AM masking effect for the intermediate color, yellow. Because AM masking was not found for

any of the other target colors when a red/green pair was used, it should be noted that this result is also consistent with the possibility that not only was an intermediate color not interpolated, but none of the AM-inducing colors was represented on the AM path under such conditions.

Second, it is possible that interpolation of color along the AM path was not observed in previous studies due to luminance cues. Souto and Johnston (2012) found that color masking on the AM path only occurs when the targets are isoluminant with the background. They further suggest, based on early work (Dimmick, 1920; Wertheimer, 1912), that luminance information dominates long-range apparent motion. In line with this, a recent study by Nagai, Beer, Krizay, & MacLeod (2011) shows that such luminance cues (brightness) can indeed be integrated in long-range apparent motion when the inducers with different luminance were perceived as the same object. Thus, it may be that intermediate colors can be represented along the AM path only when luminance information in both inducers and targets is excluded as in the current study.

Another difference can be found in the psychophysical methods used to probe illusory representations in each study. Kolers and von Grünau (1976) used a matching technique, in which observers were asked to match the illusory color they perceived in the apparent motion path with the physically presented color. Appearance of illusory color in the periphery, if perceived, could be different from the appearance of the matching stimulus that is physically presented near fixation (McKeefry, Murray, & Parry, 2007). A recent study from Souto and Johnston (2012) used a similar 2AFC task to ours, measuring sensitivity to detect differently colored targets. However, this study did not explicitly test a possible intermediate color between red/green stimuli (yellow).

In addition to the AM-induced masking effect for the intermediate color (cyan), we also replicated the previous findings showing AM masking for the terminal color (green) in Experiment 1. This result may be accounted for by predictive updating of color before the terminal inducer is presented as suggested previously (Kolers & von Grünau, 1976). However, when orange/magenta (Experiment 3), green/orange (Experiment 4), and red/green (Experiment 5) pairs were used, none of the terminal colors (magenta, orange, and green, respectively) showed a significant AM-induced masking effect compared to a control color failing to confirm predictive updating of color in AM.

Previous behavioral work has demonstrated that color mixing can occur over a short distance in motion, suggesting that color of moving objects can be spatiotemporally integrated into moving stimuli along the motion trajectory (Nishida, Watanabe, Kuriki, & Tokimoto, 2007). However, since the distance between our apparent motion inducers and the target is over 2°, which largely exceeds the distance used in their study (3–12 min), our results are not likely to be accounted for by the same mechanism of color mixing. Also, the intermediate colors (cyan, pink, and lime) based on averaged cone-contrast are not always the same as the additive color mixture of two inducing colors (blue/green, orange/magenta, and orange/green, respectively). Furthermore, when the intermediate color was chosen based on the additive color mixture (individually set yellow from a red/green pair) instead of based on cone-contrast in Experiment 5, we did not observe a significant AM masking effect for the intermediate color, yellow, indicating that an interpolation in the color representation, as shown in shape (Kolers & von Grünau, 1976) and orientation (Chong, Yu, & Shim, 2012), rather than color mixing, is responsible for the results shown in the current study.

It is possible that increased attention to the apparent motion path causes decreases in the detection thresholds for the on-path targets compared to the off-path targets. However, it is unlikely that this attentional difference can account for the AM masking effect for the intermediate color; while the attentional difference between On-path and Off-path is likely to cause a change in detection thresholds for all four target colors, we found a selective threshold elevation only for the intermediate colors (cyan, pink, and lime) and one of the terminal colors (green in Experiment 1).

One consequence of the cone-contrast based color choice in the current study is that, the intermediate colors (cyan, pink, and lime) have cone-contrast with the EES "white" background in only one chromatic channel (e.g., cyan and pink: only L-cone contrast, lime: only S-cone contrast) whereas initial and terminal colors have cone-contrast with the background in both chromatic channels. Thus, one may argue that the elevated detection threshold for the intermediate colors can result from this signal difference. However, this is not likely to be the case since the threshold elevation for the intermediate colors was observed only when the colors were presented on-path, but not when they were presented off-path. Furthermore, the threshold elevation was not shown when the same color was used as a control color, indicating that the threshold elevation occurred due to color interpolation rather than due to the specificity of the intermediate colors.

Another point to note is that although we chose the target detection paradigm to avoid problems of conscious biases in subject report, similar to other recent literature on AM masking effects (Hidaka et al., 2011; Schwiedrzik et al., 2007; Souto & Johnston, 2012; Yantis & Nakama, 1998), because no appearance measure was used, such as the color matching procedure in Kolers and von Grünau (1976), we cannot

rule out the possibility that AM masking may influence target detection independent of target appearance. Future studies will be required to clarify this issue.

In line with behavioral evidence for illusory representations induced by apparent motion, several neuroimaging studies have demonstrated that the perception of AM leads to increased activation in the region of the primary visual cortex (V1) corresponding to the AM path (Larsen, Madsen, Lund, & Bundesen, 2006; Muckli, Kohler, Kriegeskorte, & Singer, 2005; but see Liu, Slotnick, & Yantis, 2004). More recent studies using electroencephalography (EEG) and dynamic causal modeling (DCM) of fMRI data suggest that this activation increase in V1 is driven by feedback signals from hMT+/V5, which has large receptive fields (Sterzer, Haynes, & Rees, 2006; Wibral, Bledowski, Kohler, Singer, & Muckli, 2009). However, since these studies did not probe how features of an object engaged in AM are represented in these cortical regions, the neural mechanisms underlying feature updating in apparent motion are presently unclear. Recently, we have shown that orientation information is represented in the region of V1 that is retinotopic to apparent motion paths when oriented gratings undergo apparent rotation (Chong et al., 2012). The updated representation of orientation on the AM path suggests a possibility that feedback from other higher order visual areas that are implicated in the processing of object shape, such as lateral occipital cortex (LOC), may play a role in these interpolation processes during apparent motion (Liu et al., 2004; Yantis & Nakama, 1998; Zhuo et al., 2003). In the case of color, however, it is not clear whether a similar feedback mechanism contributes to color updating during AM. It has been shown that the representations of color in higher order visual areas, such as human V4 and ventral occipital (VO) cortex, reflect perceptual color rather than chromatic contrast (Brouwer & Heeger, 2009). In the current study, we define colors within dimensions of Cone-Excitation color space, which is manipulating colors along chromatic channels. We found that color updating was observed only when the colors of the AM inducers varied along one dimension of chromatic channels, indicating that the representation of the updated color is more likely to be based on intermediate chromatic contrast rather than the perceptually intermediate color. This also cannot be explained by a higher order color representation such as perceptual distance between AM inducing colors. When the chromaticity values of the inducing colors are transformed to the chromaticity values in a perceptual color space (i.e., CIE Lab), the perceptual distance between green and blue (where we observed color updating) is larger than the distance between red and green (where we did not observe color updating). Our finding, thus, suggests

that the illusory color representation during AM may be reconstructed earlier than V4.

In conclusion, our study shows that intermediate colors, different from the colors of apparent motion inducers, can be interpolated when the color of an object changes during apparent motion. Together with previous studies that revealed interpolation of objects' form (Hidaka et al., 2011), this finding suggests that intermediate features can be represented in apparent motion for both form and color, presumably via similar interpolation processes.

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