

Masking and color inheritance along the apparent motion path

David Souto

Cognitive, Perceptual, and Brain Sciences,
Division of Psychology and Language Sciences,
University College London, London, UK
Faculté de Psychologie et des Sciences de l'Éducation,
Université de Genève, Geneva, Switzerland



Alan Johnston

Cognitive, Perceptual, and Brain Sciences,
Division of Psychology and Language Sciences,
University College London, London, UK;
CoMPLEX, University College London, London, UK



Long-range apparent motion is the illusory motion that can be perceived when two static and distant stimuli are presented in succession. Within some spatiotemporal range not only is motion sensed, but it appears as if one stimulus is displaced from one place to another (termed beta or optimal motion). Several groups have found that this illusory percept can interact with perception of a physically present stimulus, but some disagree on the origin of these interactions. We know little about how suppressive effects depend on feature-similarity between a target and the stimuli in apparent motion (inducers)—which would indicate an early perceptual locus—or even about the minimal conditions under which to obtain this effect. Unlike early studies that used a two-stroke apparent motion paradigm, we were able to demonstrate that motion can mask stimuli presented at interpolated locations along the apparent motion path, as shown by the elevation of contrast thresholds compared to a control condition. Apparent motion masking depended on color similarity between target and inducers. Further, we found evidence that the color of inducers alters the apparent color of intervening gray probes, indicating some inheritance or chromatic averaging across distant locations, but no clear evidence of predictive updating. Finally, the analysis of the presentation times delivering maximal masking effects suggests a predictive interpolation process is responsible for interference by apparent motion filling-in. We discuss alternative mechanisms, in particular the possible role of apparent-motion-induced metacontrast masking in generating this pattern of results.

Keywords: apparent motion, masking, filling-in, interpolation

Citation: Souto, D., & Johnston, A. (2012). Masking and color inheritance along the apparent motion path. *Journal of Vision*, 12(7):18, 1–18, <http://www.journalofvision.org/content/12/7/18>, doi:10.1167/12.7.18.

Introduction

Under continuous illumination, visual motion can be computed locally (e.g., Johnston, McOwan, & Buxton, 1992; Watson & Ahumada, 1985). Our perception of motion, however, extends to discontinuous stimulation (e.g., stroboscopic illumination) as well, within a wide spatial and temporal range—referred to as long-range apparent motion. Apparent motion percepts were essentially categorized by Wertheimer (1912) into “phi”—“objectless” or “pure” motion—and “beta” or “optimal” motion, the impression of seeing one object (the illusory “token”) move from one place to another, instead of two stationary flashes. Beta motion is of general relevance to filling-in phenomena—it can be considered as a case of spatiotemporal filling-in, generating a percept at a location in space that is not

physically stimulated (Pessoa & De Weerd, 2003). In this contribution, we ask how the impletion process in optimal apparent motion interferes with incoming visual information and, in particular, if and when the illusory token causes interference at the feature-level as a function of color-similarity with the target.

Several groups have found that apparent motion can interact with the perception of a physically present stimulus and, in particular, that the perception of stimuli presented along the apparent motion path can be suppressed (Hidaka, Nagai, Sekuler, Bennett, & Gyoba, 2011; Hidaka, Teramoto, & Nagai, 2012; Hogendoorn, Carlson, & Verstraten, 2008; Schwiedrzik, Alink, Kohler, Singer, & Muckli, 2007; Yantis & Nakama, 1998). We will argue that it is still unclear whether those effects can be found at an early perceptual processing level (Hidaka et al., 2011) and whether they invalidate arguments put forth to account

for early failures to find apparent motion masking (Kolers, 1963a, 1963b).

Different accounts of apparent motion masking have been offered. Some authors (Liu, Slotnick, & Yantis, 2004; Yantis & Nakama, 1998) have proposed that masking takes place at an object-level stage along the ventral processing stream, possibly involving the lateral occipital complex (LOC), explaining impaired discrimination of letters presented along the apparent motion path as well as the perceptual distortion and lower discrimination of simple shapes (Khuu, Phu, & Khambiyee, 2010). The fact that Attneave and Block (1974) failed to obtain masking with a similar paradigm to Yantis et al. (1998) when asking for the detection of low-contrast flashing LEDs speaks in the favor of this hypothesis, as this account would predict little effect on the detection of luminance increments.

On the other hand, Schwiedrzik et al.'s (2007) finding of better detection for targets presented in-time than for off-time targets is incompatible with a masking account and was interpreted as a consequence of predictive coding of visual information: "A target that appears in-time with the moving token would fit the prediction better than a target that will appear out of time. Therefore, it should be masked less. A spatio-temporally fitting motion stimulus on the apparent motion trace might not be masked at all (Attneave, 1974)." (Schwiedrzik et al., 2007, p. 3430).

Finally, Hidaka et al. (2011) have recently shown that apparent motion reduces detection sensitivity more when targets and inducers are oriented the same way compared to when they have different orientations, which would contradict the last proposal. They interpret this as evidence of an early visual interaction between the physical and illusory percept.

All of the previously cited experiments that have shown a masking effect along the apparent motion path have used cyclical presentations, even those that aimed to test image-level interactions (Hidaka et al., 2011; Hidaka et al., 2012). This led several authors to suggest that, with one single cycle, it would be perfectly normal to not find masking, as then motion would be detected after target presentation (Attneave & Block, 1974; Schwiedrzik et al., 2007; Yantis & Nakama, 1998), explaining the fact that an early study of Kolers failed to find apparent motion masking with a two-stroke display (Kolers, 1963a, 1963b). Another relevant factor is eccentricity. Hidaka et al. presented stimuli at 5, 10, and 15° of eccentricity, and their effect seemed most robust at 10°, while Kolers presented stimuli parafoveally. However, apparent motion is also observed foveally and parafoveally. If a condition for apparent motion masking was peripheral presentation, it could indicate that other factors may be implicated, such as the motion-induced mislocalization of features (e.g., Khuu, Kidd, & Errington, 2010). We aimed to study masking in

conditions similar to the study of Kolers to understand the limiting conditions of apparent motion masking.

Is apparent motion masking like simultaneous pattern masking?

In order to understand low-level interactions involved in apparent motion masking, we need to also take into account the effects of backward masking or metacontrast. Metacontrast has long been considered to be related to apparent motion, as apparent motion (typically split-motion) and metacontrast—the suppression of the first presented stimulus by a nonoverlapping subsequent stimulus—co-occur over a wide range of stimulus parameters (Fisicaro, Bernstein, & Narkiewicz, 1977; Kahneman, 1967; Stoper & Banffy, 1977; Weisstein & Growney, 1969).

The previously cited experiments control for metacontrast by either having a "flicker" condition or a condition in which only the terminal stimulus is shown. Spatial separation is another factor that can differentiate the apparent motion masking effect from metacontrast masking. Some authors report little backward masking with separations of flanking lines above 0.9°, edge-to-edge (Growney, 1977). Nonetheless, by definition, apparent motion may extend this limit by allowing perceptual integration of target and "post-mask" across space. We call this *apparent-motion-induced* metacontrast masking (backward masking for simplicity). In that case, instead of attributing masking to the contemporary presentation of the target at the place and time at which the trajectory is filled-in, we attribute masking to interference between the target and the second stimulus presentation in a way that depends on grouping by apparent motion, but does not have to be constrained by a specific apparent motion trajectory.

Recent experiments have shown that color and luminance can be integrated in long-range apparent motion (Nagai, Beer, Krizay, & Macleod, 2011; Nagai, Kimura, & Nakauchi, 2011). The reduction in the detection of color change between two inducer locations was taken as an indication of integration, similar to that found in short-range apparent motion displays (Nishida, Watanabe, Kuriki, & Tokimoto, 2007; Watanabe & Nishida, 2007). Here, we used color to assess feature-specific masking and how object color is updated along the apparent motion path. We can use updating of information between inducers to tackle the distinction between backward interference (apparent-motion-induced metacontrast) and simultaneous interference.

Concerning masking, more precisely, our hypothesis was that, if apparent motion filling-in interferes with the visual processing of a target presented in its path, this process should be demonstrable through an interaction between the features of the target and of

the inducers generating apparent motion. Apparent motion masking may then be equivalent to a simultaneous version in which a target is masked by the background (Legge & Foley, 1980)—simultaneous masking. Within this framework, masking would be an index of the strength of filling-in due to spatiotemporal interpolation. This means that the function relating target threshold to illusion strength could be a dipper function, i.e., facilitation is obtained with very low contrast masks over a narrow contrast range. Therefore, the presence of a suppressive effect would indicate that the mask—here, the filled-in trajectory—possesses a high enough (subjective) contrast to have a suppressive effect on the target, overcoming the dip.

This interaction would be consistent with Hidaka's and Kolers' account of apparent motion masking, attributing masking to a lower-level interaction between filling-in and incoming information. It also generates opposite predictions to the account of Schwiedrzik et al. (2007).

If we were to make a strong test of the interaction between apparent motion filling-in and the detection of light increments, masking should also be found under conditions of reduced external uncertainty and parafoveal presentation. The randomization of target location along the apparent motion path and temporal uncertainty, used in cyclical paradigms, may amplify the masking effect but should not be a necessary factor. In our paradigm, observers knew when the target was going to be presented and at which location along the apparent motion trajectory. Our first motivation has been to tackle early mechanisms in play in apparent motion masking. Failures to observe masking under those conditions would be inconsistent with a low-level (feature-level) interaction account.

In a series of six experiments, we explored the effect of apparent motion, as generated by a two-stroke display on contrast threshold for perceiving a light decrement (Experiments 1, 2, 4–6) and on the appearance of suprathreshold targets (Experiment 3).

In Experiment 1, we wanted to test the existence of color-specific masking, which would suggest an early-level interference along the apparent motion path (Hidaka et al., 2011). A further aim was to test whether the illusory color is updated along the apparent motion trajectory when inducers have different colors. In Experiment 2, we tried to ascertain the existence of color-specific masking by adjusting inducers distance individually (as in Experiments 4–6) and by using isoluminant targets. In Experiment 3, to further test whether the motion token color is updated along the apparent motion trajectory we exploited the fact that, in Experiment 1, suprathreshold targets appeared to inherit the color of inducers.

The simultaneous masking account would require maximal masking when the presentation of the target

coincides with the presence of the illusory token. A backward masking account would predict maximal masking near the presentation of the terminal stimulus. We found confirmation of the first proposal by varying the presentation time of the target in Experiment 4.

We ran two further controls. In one, we aimed to explain why earlier studies (Kolers, 1963a, 1963b) found no masking under comparable conditions by testing whether the effect can depend on the use of soft-edged versus hard-edged stimuli (Experiment 5). In the last control, we compared a flicker and apparent motion condition (inducer-target-inducer) to a more classical metacontrast condition (target-inducer) (Experiment 6), showing much larger masking in the apparent motion condition than in a flicker or metacontrast condition.

General methods

Subjects

Seven young adults participated in Experiments 1, 2, and 3, and eight participated in Experiment 4, including one of the authors (DS). In Experiments 1 and 2, six experienced observers were tested, three in Experiment 3, and five in Experiment 4. The remaining observers were undergraduates at the University College London, who were paid £6 an hour for participating. All subjects reported normal or corrected-to-normal vision.

For practical reasons, Experiments 5 and 6 were run at the University of Geneva. Twelve young adults, undergraduate students of the University of Geneva and author DS took part in Experiment 5. Ten undergraduate students of the University of Geneva and author DS participated in Experiment 6. Students received course credit for participation. Procedures adhered to the tenets of the Declaration of Helsinki.

Stimulus generation and materials

Stimuli were displayed on a Mitsubishi Diamond 230 CRT screen with a 100 Hz refresh frequency and a resolution of 1024 × 768 pixels. Observers sat in a dimly lit room at a viewing distance of 57 cm from the screen. Their heads were stabilized with a head and chin rest. Stimuli were generated using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) within MATLAB (The MathWorks, Inc.). In Geneva, the setup was slightly different. The CRT screen resolution was 1280 × 1024 pixels (NEC MultiSynch) with a refresh frequency of 85 Hz.

Data analysis

We first tested the statistical significance of different factors by running a repeated-measures analysis of variance. We then ran multiple two-way paired *t*-tests, comparing between particular conditions. We controlled for the false discovery rate by using the Benjamini-Hochberg method (Benjamini & Hochberg, 1995). Only the corrected *t*-test values are reported.

Experiment 1: masking along the apparent motion path

In the first experiment, we wanted to test apparent motion masking for different locations along a hypothetical apparent motion path. We tested whether masking depended on the similarity between target features and inducer features by varying the color of the targets. Our rationale was that, for instance, red targets might be harder to detect against a red background generated by apparent motion filling-in. Inducers alternated in color (either red to green or green to red) as in the classical study of Kolers and van Grunau (1976). In this study, observers had to rate the color of the illusory object token at different locations. It was found that tokens seemed to take the color of the upcoming stimulus somewhere between the two inducer locations.

The choice of temporal and spatial separation between inducers was guided by previous studies (e.g., Burt & Sperling, 1981; Gepshtein & Kubovy, 2007; Schwiedrzik et al., 2007; Yantis & Nakama, 1998) with the constraint that there was no spatial overlap between the target and the inducers.

Methods

Stimuli and materials

Figure 1a shows the stimuli and the time-course of a trial in the apparent motion (AM) and Flicker conditions. At the beginning of a trial, the fixation spot (0.3° diameter) was on for 0.5 s. Two identical pairs of inducers were presented on both sides ($\pm 3^\circ$ horizontally) of the fixation spot. In the AM condition, a Gaussian blob was presented for 100 ms and then 80 ms (ISI); later, a second blob was presented vertically displaced by 3.6° (center-to-center) upward. Thus, apparent motion was always experienced upward. In the Flicker condition, the upper and lower blobs were shown simultaneously on both sides for 100 ms and again 80 ms later.

Additionally, a target was presented either to the right or left of fixation at different locations in space-time after the offset of the first stimulus, as shown in

Figure 1b. Targets presented with an ISI of 20 (P1), 40 (P2), or 60 ms (P3) were respectively located at 2/5, 3/5, or 4/5 of the distance between inducers, going upward. Inducers and targets had a Gaussian-windowed luminance profile with a standard deviation of 0.37° and a maximal luminance of 20 cd/m^2 . Stimuli were displayed over a gray background of 41 cd/m^2 . The CIE (1931) *xy* color coordinates of the red and green stimuli we used are displayed in Figure 2. They were set at the limits of the gamut of the monitor (Red: $x = 0.62$, $y = 0.33$; Green: $x = 0.28$, $y = 0.59$).

Procedure

Weber contrast thresholds for the detection of a target located in the apparent motion path were measured by using a 2AFC task. Here, Weber contrast represents the normalized maximal difference in luminance intensity between the stimulus and the mean luminance of the background $(I_{\text{max}} - I_{\text{background}}) / I_{\text{background}}$. Observers had to report on which side of the fixation spot the target was presented by pressing the left or right arrow key on the keyboard. The threshold contrast generating 82% correct answers was estimated for each target color using the QUEST adaptive procedure (Watson & Pelli, 1983). This estimation was based on 50 trials. Each trial was self-paced, starting as soon as a response was provided.

The experiment was run in two sessions, each with a different alternation of the green (G) and red (R) blob (G→R and then R→G). The experimental design was within subject with factors Presentation (AM, Flicker) × Inducers Color (G→R, R→G) × Target Position (P1, P2, P3) × Target Color (R, G) × Target Side (left, right). Target Side and Target Color were randomized within a block. Within a session, the same block order was used for each subject, alternating AM and Flicker conditions from one block to the other (Flicker, P1; AM, P1; Flicker, P2; AM, P2; Flicker, P3; Flicker, P3). Each session started with 20 training trials. There were 50 trials per condition, disregarding Target Side.

Predictions

We illustrate in Figure 1c the hypothetical form of perceptual interpolation (apparent motion) that may take place between inducers. We hypothesized that the apparent motion filling-in process might have a similar effect on the detection of a target presented in the apparent motion path as a physical background. When this background (or pedestal) is similar in color or luminance to the target contrast, we can expect an elevation of thresholds. Thus, if red was filled-in along the motion trajectory, we expect red targets to be harder to detect against this induced illusory red

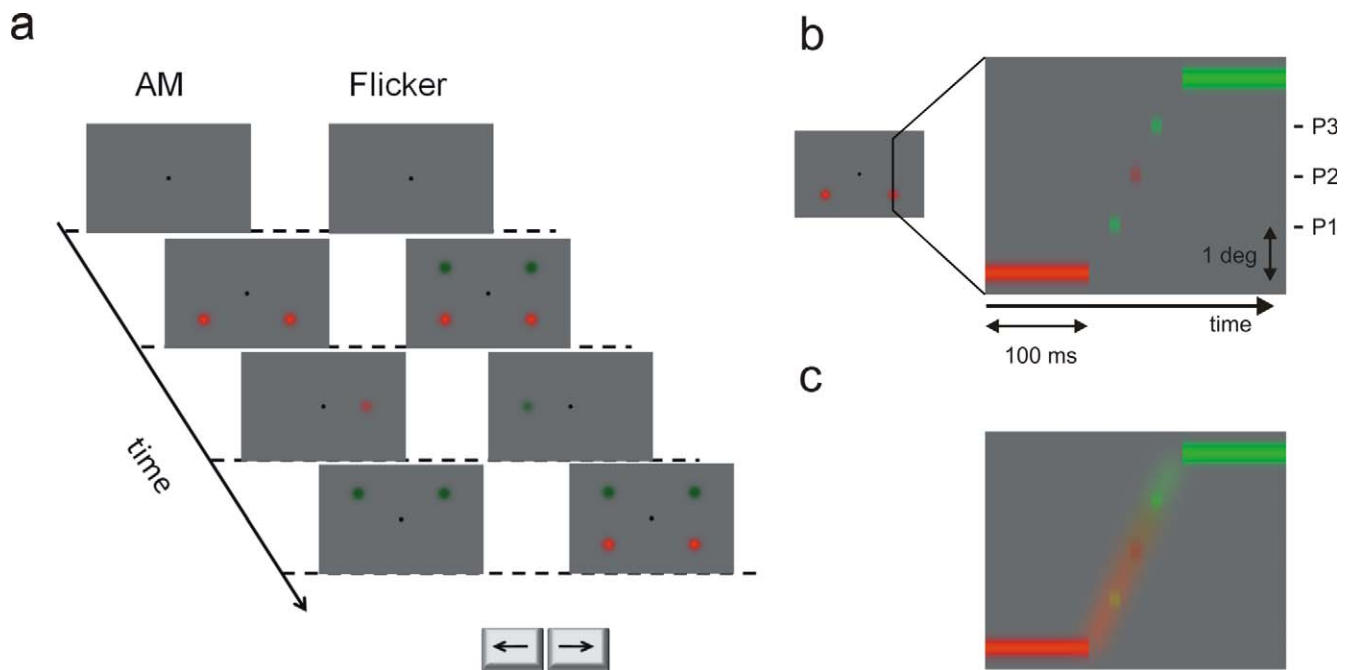


Figure 1. (a) Screen captures showing the event sequence in Experiment 1 AM and Flicker conditions. Only the central part of the screen is shown. In the AM trial, a red target is shown on the right side; a green target is shown on the left side in a Flicker trial. At the end of the trial, a directional response is required to locate the side that contains the target. (b) Space-time plot for an AM trial, showing a pixel column cutting through the middle of inducers across time. All possible target locations and colors are shown. Panel (c) represents possible subjective filling-in induced by apparent motion. Due to filling-in, red targets may become harder to detect, because they are seen over a red background—in the beginning and middle of the trajectory—while green targets may be harder to detect because they are seen over a green background at the end of the apparent motion trajectory.

background, delivering higher contrast thresholds (Figure 1c). The same applies for green targets.

The flicker condition is intended to control for possible effects of long-range interactions. In fact, this experiment and the following will show that there is very little influence of flickering stimuli on target contrast thresholds, even with short spatial separations.

Results and discussion

The main results of Experiment 1 are shown in Figure 3. First, it is apparent that, although we find masking effects, i.e., an elevation of thresholds in the AM compared to the Flicker condition, those largely depend on the position of the target and to a lesser extent on its color. Note that, due to the use of a fixed distance between stimuli in apparent motion, we were unable to obtain contrast thresholds for as many as seven participants, especially for the last location, who were therefore not included in the group analysis. They reported they could not see the target, especially for the last location (P3). The effect of apparent motion masking is therefore underestimated in this experiment.

Masking effects increase as we approach the second inducer position. This is clear from a comparison of the

second (P2) and third target position (P3), less so for the first (P1) compared to the second target position. Further, contrary to our expectations, we found no dependence whatsoever of target detection on inducers color. The only notable, and unexpected, effect of target color that we found was that green targets led to higher thresholds in the AM condition compared to the Flicker condition.

A repeated-measures ANOVA (Presentation \times Inducers Color \times Target Color) on contrast thresholds confirmed a significant main effect of Presentation ($F[1, 6] = 28.26, p < 0.002$), indicating an apparent motion masking effect, Position ($F[2, 12] = 18.1, p < 0.001$), Target Color ($F[1, 6] = 17.45, p < 0.01$), an interaction between Presentation and Target Position ($F[2, 12] = 43.33, p < 0.001$), indicating increased masking for targets near the second location, and between Presentation and Target Color ($F[1, 6] = 15.10, p < 0.01$), indicating that green targets were more masked by apparent motion than red targets (0.08 versus 0.04 threshold elevation, two-tailed, $t[6] = 3.89, p < 0.01$).

Masking of a target presented on the apparent motion path seems to contradict previous reports using two-stroke apparent motion (Kolers, 1963a), with a separation of 2.65° . The absence of masking by long-range apparent motion was, at that time, seen as a

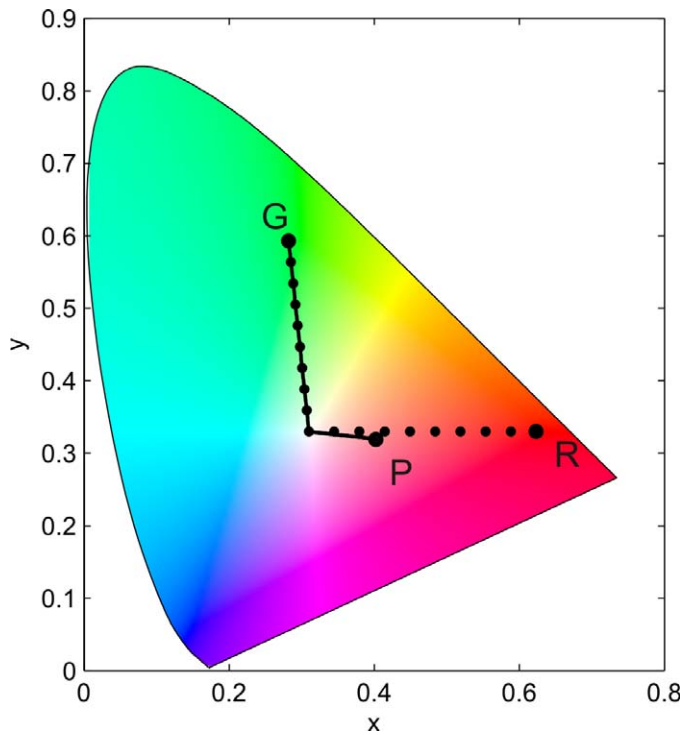


Figure 2. Color axis used in Experiment 2 to vary the saturation of pink and green targets. The dots indicate the target colors used in Experiment 3. The red (R), pink (P), and green (G) inducer colors are at the end of each axis. Of note, colors in the diagram are provided for illustration as the rendering is display-dependent.

fundamental difference between long-range apparent motion and physical (continuous) motion, as it was found, using a similar paradigm, that a flashed target was strongly masked by a stimulus in real (unsampled) motion (Luria, 1965). We speculate that the lack of masking by apparent motion may be due to the stimuli used—sharp-edged inducers and sharp-edged, high-contrast targets (see Experiment 5). Indeed, sharp-edged inducers are less likely to generate optimal motion (von Grunau, 1978).

In our context, the effect of target location on apparent motion masking indicates a discontinuous filling-in process with stronger masking for targets appearing near the second stimulus. This is reminiscent of the partial-motion percept—the illusion of seeing a displacement of the object token for only a part of the trajectory—that is likely to be obtained with certain stimulus parameters, but the occurrence of which is very variable among subjects (e.g., Ekroll, Faul, & Golz, 2008). Further, we presented the targets at specific times and locations, making the assumption that the interpolation process is linear (see Figure 1c). This may not be the case, and thus perception could be facilitated when the target presentation is offset from the actual interpolated path.

The interaction between Target Color and Presentation was unexpected. While both target colors seem

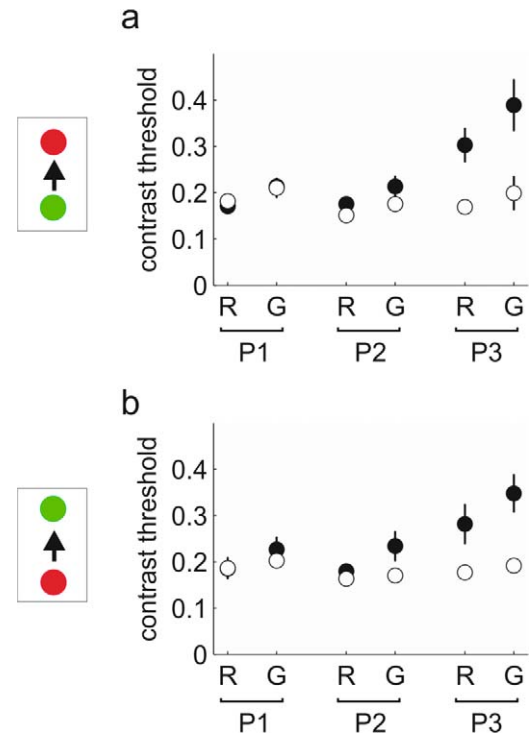


Figure 3. Experiment 1: Luminance contrast thresholds for the detection of a red (R) or green (G) target presented along the apparent motion path (positions: P1–P3). Apparent motion (AM) and Flicker conditions are shown in filled and open symbols. Error bars represent between-subjects SEM ($N = 7$).

equally detectable in the Flicker condition, detection was substantially different in the AM condition. Green targets were more masked by apparent motion (AM minus Flicker threshold) than red ones. As the difference arises only in the AM condition, it seems plausible that temporal properties of green and red color processing could account for the difference. Because we flash a target for a brief period of time, the shorter the visual persistence of the target, the more likely it is to be masked by apparent motion. The critical flicker fusion frequency for modulations of green patches is higher than for modulations of red patches, indicating that the response of the medium wavelength pathway has a sharper temporal impulse response than the long wavelength pathway (Giorgi, 1963; Hamer & Tyler, 1992; Landis, 1954), lending support to the latter hypothesis.

Finally, we found that Inducer type did not interact with Presentation type. We expected thresholds to reflect the phenomenological experience of a colored stimulus moving in space, and therefore that detection would depend on the color-similarity of the target and the impleted stimulus. However, our first experiment might not have been ideally suited to test this effect. In this task, detection might be based mostly on the target luminance contrast rather than its color. Further, when reaching the

threshold luminance contrast, differences in color between a red and a green patch can hardly be resolved (Finkelstein & Hood, 1984) and therefore no strong color-specific masking can be expected in this experiment.

Experiment 2: isoluminant targets

The absence of color-dependent masking may indicate detection based on luminance rather than hue. Therefore, in [Experiment 2](#), we used colored targets that were isoluminant with their background. Also, we individually adjusted the distance between inducers to optimize masking effects.

Methods

Visual stimuli

Inducers and targets were similar to the ones displayed in [Experiment 1](#) except for their hue, the distance between inducers, and the fact that targets were isoluminant with the background. To allow variations in saturation, the color coordinates of the stimuli had to be adjusted. The luminance of the background was lowered to 20 cd/m². Inducers and targets, at their highest saturation, were either pink (CIE x : 0.40, y : 0.32) or green (CIE x : 0.28, y : 0.59). Inducers were brighter than the background at 25 cd/m². In the new procedure, the target saturation (distance to the white point) was varied rather than its luminance contrast. Target saturation was expressed as a fraction of the highest saturation ($S_{\text{target}}/S_{\text{max}}$), with color coordinates lying along an axis going from the white point to the color coordinates of the fully saturated pink or green (with saturation value of 1) shown in [Figure 3](#). Targets were always displayed between inducers (position P2 in [Experiment 1](#)).

Procedure

Observers completed two sessions, one with pink inducers and another with green inducers. We tried to equate the illusion strength for different inducers and subjects by adjusting the distance between inducers. Each session started with 20 training trials followed by a threshold procedure using a target of the same color as the inducers in apparent motion. The threshold separation of the inducers was aimed for 82% correct discrimination with a 50% saturated target was estimated. The distance was varied between 2.4° (avoiding spatial overlap between the inducing and target stimuli) and 8°. In subsequent blocks of the same session, this distance was fixed to the threshold value.

Intrasubject factors were Presentation (AM, Flicker) × Inducers Color (P→P, G→G) × Target Color (P, G) × Target Side (left, right). Different Presentation and Target Color conditions were run on different blocks in a fixed order (Flicker, P; AM, P; Flicker, G; AM, G). There were 60 trials per block.

Results and discussion

[Figure 4](#) shows the average saturation thresholds as a function of target color and inducer color for seven observers. The distance between inducers determined by the threshold procedure was on average very similar for different colors of the inducers: 6.8° for pink and 7.0° for green. We found higher saturation thresholds—by about 20%—in the AM compared to the Flicker condition for targets that had the same color as the inducers, but none whatsoever when their colors differed. This conforms to our predictions ([Figure 1c](#)) that apparent motion filling-in would increase the saturation thresholds depending on the color of the inducers, in a similar way as in a simultaneous condition in which targets would have to be detected against a background of the same color. Further, we were able to approximately equate the visibility of green and pink targets as indicated by their similar thresholds in the Flicker condition—only a slightly lower saturation was needed to discriminate between green target present and target absent sides.

Separate repeated measures ANOVAs were run for different colors of inducer. The interactions between Presentation and Target Color were significant for both colors of inducer (Pink: $F[1, 6] = 10.08$, $p < 0.02$; Green: $F[1, 6] = 31.90$, $p < 0.002$), accounting for the main effect of Presentation (Pink: $F[1, 6] = 6.2$,

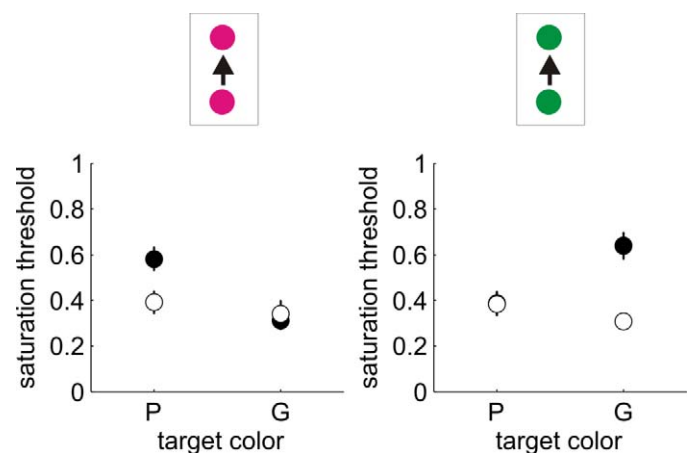


Figure 4. Target saturation thresholds as a function of inducer color (insets) and target color (pink, P, or green, G) in [Experiment 2](#). Filled and open symbols represent AM and Flicker conditions. Error bars represent between-subjects SEM ($N = 7$).

$p < 0.05$; Green: $F[1, 6] = 10.28$, $p < 0.02$) and Target Color ($F[1, 6] = 6.1$, $p < 0.05$; $F[1, 6] = 7.28$, $p < 0.05$). Post-hoc t -tests confirmed a significantly larger masking effect (AM minus Flicker) for same-color compared to different-color targets for both pink ($t[6] = 3.17$, $p < 0.02$) and green inducers ($t[6] = 5.65$, $p < 0.002$).

A limitation of the present paradigm is that, although we aimed to optimize masking effects by varying the distance between inducers, the relation between distance and optimal apparent motion may not be linear. That is, for a given temporal separation, larger distances may generate less compelling apparent motion (Gepshtein & Kubovy, 2007). Therefore, a more lengthy procedure in which perceptual performance at each distance is characterized may have led to larger effects.

To summarize, we obtained a substantial suppression when targets were of the same color as the stimuli in apparent motion but not when colors differed. We thus demonstrated the color-specificity of apparent motion filling-in and confirmed the fact that apparent motion masking can be robustly obtained with a two-stroke apparent motion paradigm. That is, the perception of a physically present target can be suppressed by the object token in apparent motion in a feature-specific way, not just a location-specific way.

Experiment 3: color-inheritance along the apparent motion path

When running [Experiment 1](#), we noticed that apparent motion could change the apparent color of some above-threshold targets. For instance, green inducers seem to make the target appear greener. Only recently has it been shown that apparent brightness can be averaged across locations undergoing long-range circular apparent motion (Nagai, Beer et al., 2011). We took this as an opportunity to measure how color is updated along the apparent motion trajectory in another way (Kolers & von Grunau, 1976). By this means, we may reveal further properties of the apparent motion filling-in process that we could have missed by using targets at threshold (cf. discussion of [Experiment 1](#)). Of interest, summation with the terminal stimulus would be predicted by a metacontrast masking account (Burr, 1984). Metacontrast would have a postdictive effect on color judgments, especially near the terminus location—a probe should appear to have a color more similar to the terminus, instead of being similar to the first stimulus. The same would happen if there was predictive updating of the token color along the apparent motion trajectory (Kolers &

von Grunau, 1976) based on the fact that the terminus color is known in any given block.

Mixing of color along the trajectory of an object in apparent motion has been recently shown for short separations between stations in space and time (Nishida et al., 2007; Watanabe & Nishida, 2007). In that case, the fusion of alternated colors can be almost as perfect as for a stationary heterochromatic flicker. This does not seem to be the case in our paradigm. Our subjective experience was that targets never appeared yellow when a red inducer was followed by a green target, indicating that the influence of motion on the integration of colors might be of a different nature for different stimulus separations.

This effect is also reminiscent of feature attribution (or feature inheritance) of vernier offsets in apparent motion (Breitmeyer, Herzog, & Ogmen, 2008; Otto, Ogmen, & Herzog, 2006). A target color change can also be attributed to further locations along an apparent motion trajectory. When a shrinking or growing bar is translating in apparent motion and one of the bars is of a different color, the colored bar is attributed to an object ahead of the trajectory, both in terms of position *and* size (Cai & Schlag, 2001). Those effects have been observed with small temporal and spatial intervals. However, to our knowledge, color inheritance is not documented for long-range apparent motion with the exception of the visual saltation illusion (e.g., Khuu, Kidd et al., 2010). In the visual saltation illusion, a series of stimuli flashed at the same location in the periphery (15°) are misperceived to move in the direction of the last flash. In that situation, the color of the mislocalized flashes can appear to be mixed (Lewis & Khuu, 2010). Unlike Watanabe and Nishida, we are unable to predict the appearance of the target resulting from a mix between real and illusory colors, because we can only indirectly infer the properties of the illusory color in a particular condition. We simplified the problem by asking observers to judge the appearance of gray targets on a red to gray and gray to green scale. The experiment is, therefore, silent regarding the question of whether the effect is akin to feature-attribution (targets taking the color of the inducers) or color averaging (targets color appearing as a mix of inducers color) between the moving object token and the target. However, we may be able to tell which color dominates at different locations along the apparent motion path when colors of the inducers alternate or stay the same, as in [Experiment 1](#).

Methods

Visual stimuli

Stimulus characteristics were similar to [Experiment 1](#). Here, the inducers were shown on only one side of the fixation point; the target had a constant contrast of 80%; there was no Flicker condition; and there were

conditions in which inducers had the same color. The side on which the inducers were presented and target color saturation were randomized within a block. One second after the offset of the second inducer, a saturation scale (14° horizontally \times 1.8° vertically) was shown 6° above the fixation point. The scale displayed 19 color saturation levels going from green to gray and from gray to red (CIE xy coordinates are shown in Figure 2).

Procedure

On half of the trials, the target was gray; in the other half the target was any color in the saturation scale except gray. This second set served as catch trials. After stimulus presentation, observers reported the appearance of the target by adjusting the position of a pointer using the left/right arrow keys. The observers were instructed to use the upward arrow key to repeat the trial if they did not see the target or were unsure about the color. The downward arrow key was used to record the judgment. The next trial started 1.5 s after a judgment was recorded. Within-subject factors were Inducers Color (R→R, G→G, R→G, G→R) \times Target Position (P1, P2, P3) \times Target Color (gray or one of 18 saturation levels from red to green) \times Stimulus Side (left, right). Inducers Color and Target Position were blocked variables. The experiment was completed in two sessions, with the same order, with a succession of blocks with the same inducers color (R→R, G→G, R→G, G→R) at three different locations (P1, P2, then P3). There were 20 trials per condition of which 10 were gray target trials.

Results and discussion

As we used the same inducers in Experiment 1, it could be that subjects did not see the target at full contrast in the P3 position. Therefore, we discarded subject observations if they were unable to respond on more than 30% percent of the trials for any given target location. The remaining subjects discarded on average 5%, 4%, and 9% of trials for P1–P3 respectively. As in Experiment 1, not all subjects could see the target at all positions, so data from seven out of 12 observers were included in the analysis. Also, because targets were suprathreshold, we were at risk that the target color may have an effect itself on the process of color-interpolation. For this reason, we only analyzed trials in which the target was gray.

Figure 5 displays the average appearance judgments by inducer color and target position. The main finding is that the perceived color of the target is biased toward the color of the first inducer (redder for R→R and R→G, and greener for G→G and G→R). However,

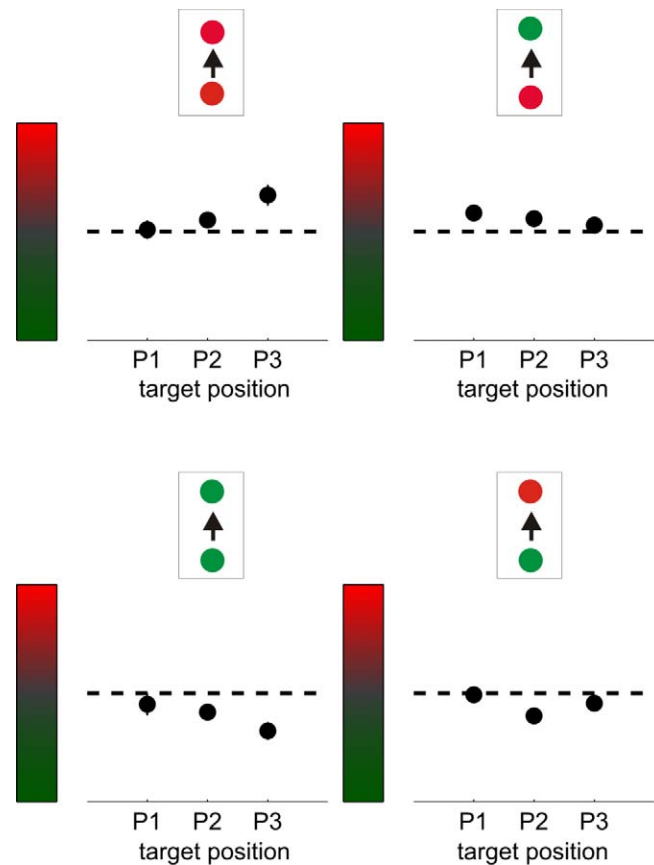


Figure 5. Experiment 3: Apparent color of a gray high-contrast target presented along the apparent motion path—with the same inducers as for Experiment 1. Error bars represent between-subjects SEM ($N = 7$).

when the colors are alternated, targets at the end position are perceived as gray instead of inheriting the color of the second stimulus.

For statistical analysis, we assigned numbers to the colors in the saturation color scale (-10 to $+10$ from green to red) and ran a repeated-measures ANOVA on the average values with the factors Inducer Color (R→R, G→G, G→R, R→G) and Position. The analysis showed a main effect of Inducer Color ($F[3, 18] = 7.44, p < 0.002$), Position ($F[3, 18] = 8.82, p < 0.004$), and an interaction between Inducer Color and Position ($F[6, 36] = 8.85, p < 0.001$), which could be due to more biased estimates at the last position for same-color than for alternated-color inducers (R→R versus R→G and G→G versus G→R). To clarify the meaning of this interaction, we ran two separate ANOVAs that tested the effect of the color of the second inducer (R→R and R→G for one; G→G and G→R for the other) and the effect of target position. Both showed a significant interaction between Inducer Color and position ($F[2, 12] = 6.57, p < 0.02$ and $F[2, 12] = 9.04, p < 0.01$), which could indicate more biased judgments for the second and especially for the last

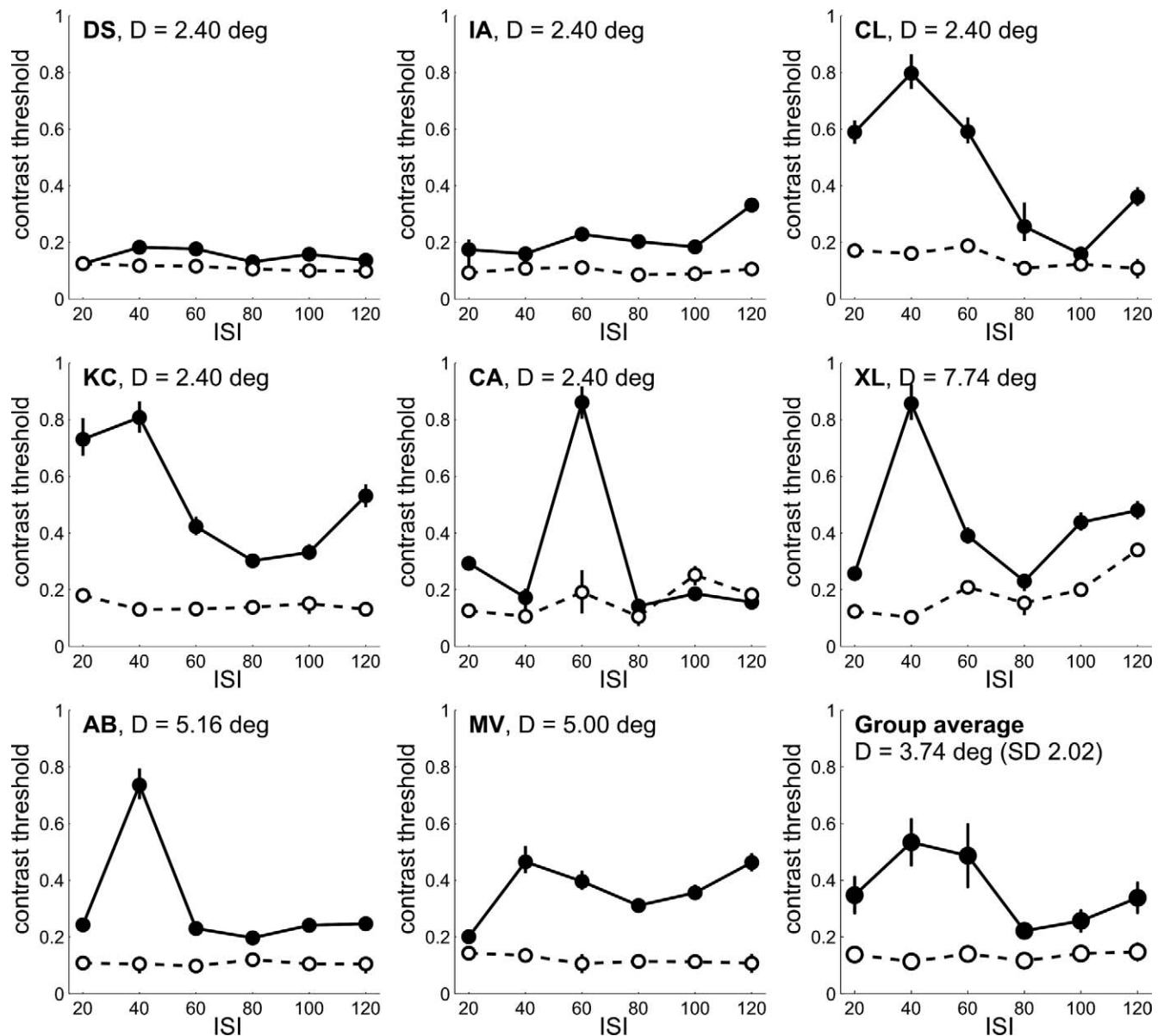


Figure 6. Target contrast thresholds as a function of Presentation condition (AM versus Flicker) and ISI for each subject in Experiment 4. Filled symbols represent AM conditions, and open symbols represent Flicker conditions. Error bars represent the 95% confidence interval containing the QUEST threshold estimate, except in the lower right panel showing the group average, where error bars stand for between-subjects SEM.

location with inducers of the same color. Using a conservative criterion (i.e., after controlling for the false discovery rate), *t*-tests showed that targets appeared significantly greener in the last position with green inducers ($p < 0.02$) and significantly greener for the second position with the green to red inducers ($p < 0.05$). However, for any given location, the comparison between Inducer conditions (R→R versus R→G and G→G versus G→R) did not reach significance.

Therefore, perceptual judgments furnished no indication that the color of the upcoming stimulus (the second inducer) was attributed to the target as we would have expected from a process of interpolation of

feature information. This would be analogous to the interpolation of object-position in apparent motion. Rather, when perception was biased, targets inherited the color of the first inducer. That is, observers tended to see greener targets when the pair of inducers was green, especially when presented at locations near the endpoint of the apparent motion path. Based on the classical study of Kolers and von Grunau (1976), we would have expected an indication of feature interpolation, i.e., targets should appear greener when followed by a green inducer even if the first stimulus is red, at least when the target is presented on the last location (P3).

Experiment 4: best interstimulus interval for apparent motion masking

Simultaneous masking and backward masking accounts make different predictions regarding the target presentation that would maximize masking. According to our simultaneous masking hypothesis, we assumed that masking would be optimal for targets presented along a notional apparent motion path, which linearly interpolates the displacement of the inducers (Figure 1c). In Experiment 4, we systematically tested for masking effects as a function of interstimulus interval (ISI) between the offset of the first inducer and the onset of the target using achromatic stimuli. As in Experiment 2, we adjusted the distance between inducers to optimize masking effects.

Methods

Stimuli and procedure

Stimuli and procedure were similar to Experiment 2, except that targets and inducers were achromatic. Contrast thresholds were calculated for different interstimulus intervals (ISI) in AM and Flicker conditions. Each ISI (20, 40, 60, 80, 100, and 120 ms) and Presentation conditions were blocked. An ISI of 80 ms means that the target was shown at the same time as the second inducer. Presentation (AM, Flicker) conditions were alternated and ISI conditions were run in ascending order. The experiment started with 20 training trials and was completed in one single session. On the first block, the distance yielding 82% accuracy in detecting a 50% contrast target with an ISI of 40 ms (as in Experiment 2) was estimated and fixed on the remainder of blocks.

Results and discussion

Data from eight subjects out of 11 was analyzed. We failed to measure thresholds under some conditions for three of the subjects. They reported a failure to see the target at 100% contrast. Indeed, although we equated the illusion strength by adjusting the distance, it was constrained to be a maximum of 8°. Figure 5 shows contrast thresholds as a function of ISI and Presentation (AM versus Flicker). The data shows a large variability in the size of the masking effect. For some, the contrast had to be maximal for certain ISIs, while for others (DS and IA), the minimal distance still allowed them to see the target nearly as well in the AM and the Flicker condition. We can also note that there is no obvious relation between the adjusted distance

and the ISI for which we obtain maximal apparent motion masking.

With the exception of the two observers for which little masking was found overall, only one observer shows masking specifically for an ISI of 60 ms; all other observers (five) show a maximal masking with an ISI of 40 ms. Evidence therefore supports the idea that apparent motion filling-in suppresses incoming information along its path with a time course that implies linear interpolation. This can only happen if the presentation of the second stimulus is anticipated, which is allowed by the predictable positions of the inducers.

Experiment 5: soft-edged versus hard-edge stimuli

Because we tested apparent motion masking under conditions similar to a study in which no masking attributable to apparent motion was found (Kolers, 1963a, 1963b), we postulated that the use of hard-edged stimuli was a determining factor in generating masking. First, apparent motion has been shown to be less optimal with a hard-edged stimulus (von Grunau, 1978). Second, if feature-similarity is of prime importance in determining masking, the hard-edged target should be more visible against a blurry apparent motion path. These two hypotheses would predict the following interactive pattern of results: less masking with hard-edged inducers compared to soft-edged inducers and also more masking with targets similar to inducers (hard-edged inducers and hard-edged targets) compared to different. This would be consistent with the findings of Khoo, Phu, and Khambiyee (2010) that shapes are easier to discriminate along the apparent motion path when they are hard-edged.

Methods

Stimuli and procedure

We used a refresh frequency of 85 Hz instead of the 100 Hz we used previously. Consequently, we adapted the displayed durations to make them as close as possible to the ones used before. The duration of the inducer and the ISI was of 94 ms (eight frames). The duration of the target presentation was of 11.76 ms (one frame). The target appeared in the middle position at 47 ms (four frames) after the first inducer offset.

We tried to equate the apparent size of the stimulus in hard-edged and soft-edged conditions. Hard-edge stimuli were disks of 13 pixels radius (0.76°). The inset of Figure 7a shows the luminance profile of the two stimuli.

The experiment was run in one session. The procedure was the same as for Experiment 4 in other

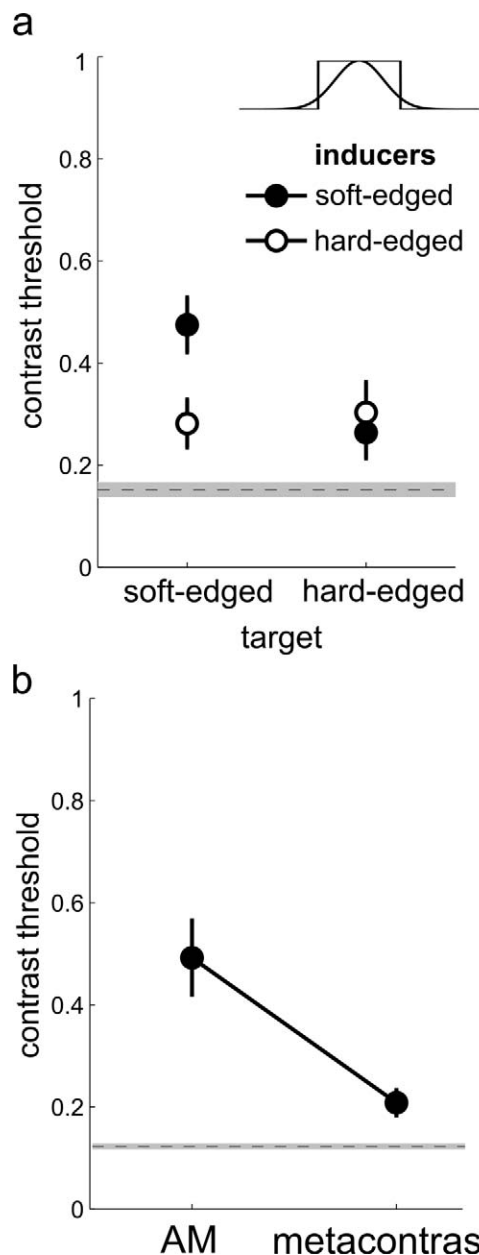


Figure 7. (a) Contrast threshold obtained in Experiment 5. Filled symbols represent soft-edged inducers, and open symbols represent hard-edged inducers. (b) Contrast thresholds obtained in Experiment 6 AM (inducer-target-inducer) and metacontrast condition (target-inducer). In both panels, the shaded baseline shows the average contrast threshold and SEM (shaded area) in the flicker condition. Error bars represent the standard error of the mean.

regards. We obtained contrast thresholds for four different blocked conditions and balanced block order across subjects.

Results and discussion

Mean distance between inducers was 5.38° (SEM 0.64°). We ran a two-factor analysis of variance (target

shape by inducer shape) on masking effect (AM contrast threshold minus flicker condition threshold). This showed no simple effect of inducer shape ($F[1, 12] = 3.242, p = 0.097$) or target shape ($F[1, 12] = 2.694, p = 0.127$). However, there was a significant interaction between those two factors ($F[1, 12] = 6.053, p < 0.05$). Post-hoc, two-tailed t -tests showed significantly higher thresholds with a soft-edged target and inducer than when the target is soft-edged and the inducer is hard-edged ($t[12] = 3.405, p = 0.005$); however, similarity to the inducer has no effect when the target is hard-edged, $p = 0.58$.

Therefore, our hypothesis was partially confirmed in that a maximal masking was found with soft-edged targets and inducers. Also we found no effect of target shape with hard-edged inducers, which could suggest that hard-edged inducers generate less optimal apparent motion (von Grunau, 1978).

Experiment 6: apparent motion masking is unlike ordinary metacontrast

An ordinary metacontrast condition would be a condition in which we present only the terminal stimulus (second inducer). It is possible that, for the last position (P3) in Experiment 1, masking was larger only because of this effect, independently of the fact that there is apparent motion between the first and the second inducer.

Methods

Stimuli and procedure

The procedure was the same as in Experiment 5. We only tested three conditions with soft-edged, luminance-defined stimuli.

We had a Flicker condition and an AM condition as in Experiments 4 and 5. We were interested in comparing this to a metacontrast condition, equivalent to the AM condition except that only the second inducer was displayed.

Results and discussion

Mean distance between inducers was 5.35° (SEM 0.44°). Figure 7b shows contrast thresholds in the AM and metacontrast condition. Although in the metacontrast condition thresholds are slightly elevated compared to the flicker condition ($+0.085$), we see a large difference with the AM condition ($+0.37$) with four times the contrast threshold in the flicker condition

(0.49 versus 0.12 contrast). We compared thresholds (Flicker versus AM, Flicker versus metacontrast) by a series of two-tailed t -tests. There was significant masking both for the metacontrast condition, ($t[10] = 3.650$, Bonferroni $p < 0.02$) and the AM condition ($t[10] = 4.896$, Bonferroni $p < 0.001$). We also confirm our hypothesis that the masking effect is not the same as an ordinary metacontrast masking effect by showing a significantly higher masking in the AM condition compared to the metacontrast condition ($t[10] = 3.656$, Bonferroni $p < 0.02$).

We therefore provide support for the idea that ordinary masking is involved in the masking effects observed, as we find a significant masking in a condition in which only the second inducer is shown. Nonetheless, masking is much more important in the AM condition, discarding ordinary metacontrast as a general explanation.

General discussion

We tested whether apparent motion filling-in interferes with the detection and appearance of a target flashed in the motion path. By placing a target along a notional, apparent motion trajectory, we expected an increase of contrast thresholds as a function of the perceptual similarity between target and impleted apparent motion percept in an analogue fashion to the detection of a contrast increment against a stationary mask (Legge & Foley, 1980).

Targets that differed in color and luminance with respect to the physical background were masked independently of their chromatic similarity with the inducers generating apparent motion. This could be due to the fact that the “filled-in” color signal was too weak to have an effect on target detection. Other authors have noted the subtlety of this percept in deciding at which point along the apparent motion trajectory the illusory object token changes color (Cowan & Greenspahn, 1995). We further questioned whether there could be any color-specific masking under conditions in which the differences in color between target and inducers are more salient, as the absence of an effect of color would be in contradiction with the phenomenological experience of a colored moving token—a colored “vehicle of movement” (Neff, 1936). However, we did find relatively large color-dependent masking effects when targets were physically isoluminant with the background. Targets of the same color as the inducers required higher saturation contrasts to be detected compared to targets of a different color (such as pink target paired with green inducers). This effect was absent when both inducers were presented simultaneously. This last result bears

some resemblance to the observation that isoluminance was found to be a necessary condition to see color drive the correspondence process in ambiguous apparent motion displays (Green, 1989).

The difficulty of finding effects of color in the presence of luminance cues is consistent with early investigations (Dimmick, 1920; Wertheimer, 1912), reinforcing the view that luminance information dominates long-range apparent motion. Those investigators questioned the very existence of colored apparent motion (Dimmick, 1920; Wertheimer, 1912). Squires (1931) later reported the clear perception of color between stations for colored inducers while the observers in Dimmick’s experiments reported a gray veil, “further reported as a ‘curtain’ or ‘film’ which is not superficial but hardly bulky” (Dimmick, 1920, p. 332). This debate exemplifies the difficulty of settling this kind of question by subjective judgments alone.

Later on, observers in Kolers and von Grunau’s (1976) experiment reported that, unlike shape, colored inducers do not appear to change color in a continuous way during apparent motion but rather seem to take the color of the second inducer in a discrete manner, somewhere along the illusory trajectory. Hence the proposal that color obeys a *digital logic*, in contrast to the *analog logic* of form (Kolers & von Grunau, 1975). On the one hand, the differences with our own results may be attributed to the discrepancies that can be found when the phenomenological properties of apparent motion filling-in are directly evaluated with appearance judgments, and when they are inferred by using performance measures (Prins & Kingdom, 2009). On the other hand, appearance judgments of the color of gray targets appearing in the path of apparent motion (Experiment 3) also showed a different picture. Although we are unable to fully account for these discrepancies, our paradigm offers the opportunity of quantifying the illusion strength for each subject, which was found highly variable—a crucial step to further investigate the impletion process that results in apparent motion.

Previous studies also reported an inability of apparent motion to suppress perception along its path (Attneave & Block, 1974; Kolers, 1963a, 1963b). Among those, the experiment of Kolers (1963a, 1963b) resembles ours. Although Kolers actually found some masking in the form of a reduction of visibility when the probe was shown nearer in time to the second inducer, he found no more masking than could be attributed to metacontrast.

We asked whether the use of sharp-edged stimuli could explain this discrepant result. Indeed, we show that the best way to show apparent motion masking is to have soft-edged inducers and soft-edged targets, indicating that this might have been a factor in previous failures to find masking. Hard edges might have been easier to detect against the blurry (shapeless) apparent

motion path than the Gaussian-windowed targets used in our experiments. In addition, it was shown that the use of sharply defined stimuli leads to less optimal apparent motion, which could be attributed to inhibitory interactions between form and motion (or sustained and transient) pathways (von Grunau, 1978).

Relation to metacontrast masking

In the first experiment, objects nearer to the second inducer were more masked. We are therefore tempted to consider apparent motion masking as a subtype of metacontrast masking, i.e., a backward masking effect in which target and mask are presented in noncontiguous locations. By comparing a metacontrast (target-inducer) and an apparent motion condition (inducer-target-inducer), we show that metacontrast could only have a moderate contribution to masking.

However, as noted in the [Introduction](#), grouping by apparent motion might also generate a backward masking effect. This would be different from the classical metacontrast paradigm but would similarly result in the suppression of information by the terminal stimulus, as opposed to simultaneous masking caused by filling-in (see also Hidaka et al., 2011).

Since Wertheimer's pioneering studies, there is a sense that apparent motion and metacontrast masking are related. In a typical metacontrast masking paradigm, a subtype of backward masking, a target followed by a mask that is not overlapping in space has a lower apparent brightness (e.g., Breitmeyer & Ögmen, 2006; Bridgeman & Leff, 1979). The model of Breitmeyer attributes metacontrast masking to the suppressive effect of transient over sustained channels (Banta & Breitmeyer, 1985; Breitmeyer & Ögmen, 2006). Since both apparent motion and metacontrast may depend on the activation of the transient channels, many conditions for optimal apparent motion are also those for obtaining strong metacontrast masking. However, the two may be manifestations of related but not identical processes, as it was recently shown that they contribute independently to the phenomenon of feature-attribution (Breitmeyer et al., 2008). If we accept a backward masking account, we may explain the elevation of thresholds by the interrupted processing of the target due to the presentation of the second inducer rather than attributing it to detection against a filled-in trajectory. Other authors have claimed that apparent motion itself is the cause of the target being *fused* with the mask (Burr, 1984). It is because the target is treated as the same object as the mask that only the last instance of the object is perceived. Therefore, the masking effect we observed would be an index of how much the target features are integrated, or fused, with the subsequent stimuli due

to apparent motion. Within this framework, fusion may be related to perceptual filling-in of the apparent motion path as both may stem from the perception of object continuity across locations.

Furthermore, perceptual grouping appears to influence metacontrast masking in a similar way to apparent motion masking. Metacontrast masking depends on color similarity of target and mask with less masking for different colors (Maeda et al., 2010; Reeves, 1981), as well as on the same or different contrast polarities (Becker & Anstis, 2004). When an effect of color was found, our apparent motion masking effects showed the same dependence. However, for durations of the target and of the mask similar to the duration of our target and of our second stimulus (100 ms), metacontrast masking remains high for a broad range of SOAs—about 30 to 80 ms (Breitmeyer, 1978), whereas the timing at which maximal masking is obtained in our experiments appears to be constrained to a narrower range of SOAs (about 20 to 40 ms; target onset to onset of the second inducer). This last point lends support to the hypothesis that simultaneous masking by filling-in is responsible for the apparent motion masking effects.

Relation to predictive coding

Using a circular (and cyclical) apparent motion display, researchers have opposed perceptual extrapolation and perceptual interpolation of object position in apparent motion (Hogendoorn et al., 2008). So far, we have only used the term *interpolation* to describe the process of filling-in of perceptual gaps in space and time. After several presentations, this interpolation process is thought to occur in anticipation of the second stimulus, as in quartet-dot displays (Yantis & Nakama, 1998); therefore, we may call this a mechanism of “predictive interpolation,” as it supposes the use of foreknowledge of presentation times to interpolate between stations. This can be contrasted to extrapolation, i.e., to fill ahead based on the past stimulus trajectory. There can be no extrapolation in our paradigm as no motion is seen before the first stimulus or beyond the second one. The timings at which we find masking are roughly consistent with the view that masking is caused by the fact that the target stimulus and the illusory stimulus are perceived at the same location, causing perceptual interference. This account suggests that the position of the illusory token is well-approximated by a linearly interpolated trajectory (as shown in [Figure 1c](#)); otherwise, there would be no overlap. However, as we previously mentioned, we cannot totally exclude an account invoking a nonclassical backward masking effect—independently of whether targets are presented on- or off-path.

Recently, Schwiedrzik et al. (2007; see also Alink, Schwiedrzik, Kohler, Singer, & Muckli, 2010) proposed that a predictive coding framework could account for apparent motion masking, according to which the neural response to a stimulus is inversely related to the stimulus predictability, or to how much a stimulus location and identity fits well with the predicted input (Schwiedrzik et al., 2007). However, the hypothesized pattern of results is opposite from what we found, i.e., more masking with “fitting” targets. Their proposal was that masking should be maximal for target features that conform less to the prediction generated by apparent motion.

Predictive feature updating

By displaying the target at different locations along the apparent motion path, we were also able to test the idea that there is a predictive updating of *features* along the apparent motion trajectory (Kolers & von Grunau, 1975, 1976). We did observe that the target could inherit the color of the stimuli in apparent motion, extending previous reports of nonretinotopic averaging of luminance (Nagai, Beer et al., 2011; Shimozaki, Eckstein, & Thomas, 1999) with long-range stimuli. However, there was no indication of predictive updating. Instead, the appearance of the probe is found to be biased toward the color of the first inducer. This can be related to the temporal freezing illusion reported by Motoyoshi (2007). In this illusion, the presence of a transient freezes the perception of a change—in color, for instance—which is otherwise perceived to be continuous. If the probe acts as a transient, it could have represented a frozen-in-time color along the apparent motion trajectory.

This notion that features, but not locations, are subject to predictive updating has a parallel in the notion of predictive updating of “attentional pointers” put forth by Cavanagh et al. to account for perceptual stability across eye movements (Cavanagh, Hunt, Afraz, & Rolfs, 2010). Apparent motion and pointer updating address a similar problem of achieving constancy across different views, whether it is due to object displacement or to different fixation episodes. In their framework, when a saccade is planned, there is a shift of attentional pointers (of perceptual resources) in prediction of the new (postsaccadic) target location on the retina. This shift only concerns positional information. It wouldn’t allow for predictive updating of target color (Cavanagh et al., 2010). Evidence that attention tracking is sufficient to generate an impression of apparent motion with ambiguous stimuli also suggests that these two mechanisms for ensuring object constancy are closely related (Verstraten, Cavanagh, & Labianca, 2000).

Relation to neural correlates of long-range apparent motion

There is ample evidence that apparent motion filling-in correlates with increased neural activity in early visual areas at unstimulated locations, supporting the idea that filling-in can interfere with incoming visual information at an early stage. Feedback from MT to V1 (e.g., Wibrals, Bledowski, Kohler, Singer, & Muckli, 2009) seems a necessary condition for this type of filling-in, as a typical V1 receptive field is too small to signal long-range apparent motion (Mikami, Newsome, & Wurtz, 1986). Optical dye imaging confirms this view by showing that the activation of a possible homologue of MT in the ferret closely precedes activation in lower visual areas. This activation in primary visual areas spreads along the apparent motion path (Ahmed et al., 2008; Deco & Roland, 2010), as in transformational apparent motion, with the line-motion illusion (e.g., Jancke, Chavane, Naaman, & Grinvald, 2004). Activation in early visual for locations along the path was also observed in various fMRI studies (Larsen, Madsen, Lund, & Bundesen, 2006; Muckli, Kohler, Kriegeskorte, & Singer, 2005; Sterzer, Haynes, & Rees, 2006) with some exceptions (Liu et al., 2004). Computational models have been proposed that can account for spatial and temporal separations giving rise to optimal motion. Under those conditions, MT can generate a “traveling wave” or “G-wave” of neural activity traveling along early visual cortex (Grossberg & Rudd, 1992). A similar analysis was proposed to account for interactions between color and motion in the line-motion illusion (Baloch & Grossberg, 1997). This last model might be able to explain how color can be spread along the apparent motion path, causing color-dependent masking and feature attribution.

Conclusions

Contrary to early accounts, we showed that masking can be found along the long-range apparent motion path with simple displays, with the condition that the target is presented at times that are coincident with a location obtained by linear interpolation of the trajectory. With stimuli isoluminant with their background, masking was observed for targets of the inducers’ color, but not when they differed in color. Further, feature-inheritance with inducers in apparent motion alternating colors showed no evidence for predictive updating of the motion token. Taken together, these data support the idea that objects in apparent motion carry their visual attributes along the motion path as if continuity was assumed, causing interference with incoming information. We can

identify distinct explanations of masking. One, favored, is based on perceptual interference (or simultaneous masking) between the filled-in stimulus and the target; another is based on a kind of metacontrast masking caused by the grouping of distant locations in apparent motion. Further research would be needed to clearly separate those two alternatives.

Acknowledgments

David Souto was funded by the Swiss National Foundation (PBGEP1125961 and 100014135374). Alan Johnston was supported by the Biotechnology and Biological Sciences Research Council. The authors would like to thank members of the Vision Lab at University College London for their participation and helpful feedback. We are also thankful to Kelly Amâncio for running experiments in Geneva and to two anonymous reviewers for suggesting [Experiments 5](#) and [6](#).

Commercial relationships: none.

Corresponding author: David Souto.

Email: david.souto@unige.ch.

Address: Faculté de Psychologie et des Sciences de l'Éducation, Université de Genève, Geneva, Switzerland.

References

- Ahmed, B., Hanazawa, A., Undeman, C., Eriksson, D., Valentiniene, S., & Roland, P. E. (2008). Cortical dynamics subserving visual apparent motion. *Cerebral Cortex*, *18*(12), 2796–2810.
- Alink, A., Schwiedrzik, C. M., Kohler, A., Singer, W., & Muckli, L. (2010). Stimulus predictability reduces responses in primary visual cortex. *Journal of Neuroscience*, *30*(8), 2960–2966.
- Attneave, F., & Block, N. (1974). Absence of masking in the path of apparent motion. *Perception & Psychophysics*, *16*(2), 205–207.
- Baloch, A. A., & Grossberg, S. (1997). A neural model of high-level motion processing: line motion and formation dynamics. *Vision Research*, *37*(21), 3037–3059.
- Banta, A. R., & Breitmeyer, B. G. (1985). Stationary patterns suppress the perception of stroboscopic motion. *Vision Research*, *25*(10), 1501–1505.
- Becker, M. W., & Anstis, S. (2004). Metacontrast masking is specific to luminance polarity. *Vision Research*, *44*(21), 2537–2543.
- Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society, Series B (Methodological)*, *57*(1), 289–300.
- Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*, 433–436.
- Breitmeyer, B. G. (1978). Metacontrast masking as a function of mask energy. *Bulletin of the Psychonomic Society*, *12*(1), 50–52.
- Breitmeyer, B. G., Herzog, M. H., & Ogmen, H. (2008). Motion, not masking, provides the medium for feature attribution. *Psychological Science*, *19*(8), 823–829.
- Breitmeyer, B. G., & Ögmen, H. (2006). *Visual masking: Time slices through conscious and unconscious vision*. New York: Oxford University Press, USA.
- Bridgeman, B., & Leff, S. (1979). Interaction of stimulus size and retinal eccentricity in metacontrast masking. *Journal of Experimental Psychology: Human Perception and Performance*, *5*(1), 101–109.
- Burr, D. (1984). Summation of target and mask metacontrast stimuli. *Perception*, *13*(2), 183–192.
- Burt, P., & Sperling, G. (1981). Time, distance, and feature trade-offs in visual apparent motion. *Psychological Review*, *88*(2), 171–195.
- Cai, R., & Schlag, J. (2001). A new form of illusory conjunction between color and shape. *Journal of Vision*, *1*(3): 127, <http://www.journalofvision.org/content/1/3/127>, doi:10.1167/1.3.127. [[Abstract](#)]
- Cavanagh, P., Hunt, A. R., Afraz, A., & Rolfs, M. (2010). Visual stability based on remapping of attention pointers. *Trends in Cognitive Sciences*, *14*(4), 147–153.
- Cowan, N., & Greenspahn, E. (1995). Timed reactions to an object in apparent motion: evidence on Cartesian and non-Cartesian perceptual hypotheses. *Perception & Psychophysics*, *57*(4), 546–554.
- Deco, G., & Roland, P. (2010). The role of multi-area interactions for the computation of apparent motion. *Neuroimage*, *51*(3), 1018–1026.
- Dimmick, F. L. (1920). An experimental study of visual movement and the phi phenomenon. *The American Journal of Psychology*, *31*(4), 317–320.
- Ekroll, V., Faul, F., & Golz, J. (2008). Classification of apparent motion percepts based on temporal factors. *Journal of Vision*, *8*(4):31, 1–22, <http://www.journalofvision.org/content/8/4/31>, doi:10.1167/8.4.31. [[PubMed](#)] [[Article](#)]
- Finkelstein, M., & Hood, D. (1984). Detection and

- discrimination of small, brief lights: variable tuning of opponent channels. *Vision Research*, 24(3), 175–181.
- Fisicaro, S. A., Bernstein, I. H., & Narkiewicz, P. (1977). Apparent movement and metacontrast: A decisional analysis. *Perception & Psychophysics*, 22(6), 517–525.
- Gepshtein, S., & Kubovy, M. (2007). The lawful perception of apparent motion. *Journal of Vision*, 7(8):9, 1–15 <http://www.journalofvision.org/content/7/8/9>, doi:10.1167/7.8.9. [PubMed] [Article]
- Giorgi, A. (1963). Effect of wavelength on the relationship between critical flicker frequency and intensity in foveal vision. *Journal of the Optical Society of America*, 53, 480–486.
- Green, M. (1989). Color correspondence in apparent motion. *Perception & Psychophysics*, 45(1), 15–20.
- Grossberg, S., & Rudd, M. E. (1992). Cortical dynamics of visual motion perception: short-range and long-range apparent motion. *Psychological Review*, 99(1), 78–121.
- Growney, R. (1977). Metacontrast as a function of spatial separation with narrow line targets and masks. *Vision Research*, 17(10), 1205–1210.
- Hamer, R. D., & Tyler, C. W. (1992). Analysis of visual modulation sensitivity. V. Faster visual response for G- than for R-cone pathway? *Journal of the Optical Society of America A. Optics and Image Science*, 9(11), 1889–1904.
- Hidaka, S., Nagai, M., Sekuler, A. B., Bennett, P. J., & Gyoba, J. (2011). Inhibition of target detection in apparent motion trajectory. *Journal of Vision*, 11(10):2, 1–12 <http://www.journalofvision.org/content/11/10/2>, doi:10.1167/11.10.2. [PubMed] [Article]
- Hidaka, S., Teramoto, Y., & Nagai, H. (2012). Sound can enhance the suppression of visual target detection in apparent motion trajectory. *Vision Research*, 59, 25–33.
- Hogendoorn, H., Carlson, T. A., & Verstraten, F. A. (2008). Interpolation and extrapolation on the path of apparent motion. *Vision Research*, 48(7), 872–881.
- Jancke, D., Chavane, F., Naaman, S., & Grinvald, A. (2004). Imaging cortical correlates of illusion in early visual cortex. *Nature*, 428(6981), 423–426.
- Johnston, A., McOwan, P. W., & Buxton, H. (1992). A computational model of the analysis of some first-order and second-order motion patterns by simple and complex cells. *Proceedings of the Royal Society B: Biological Sciences*, 250(1329), 297–306.
- Kahneman, D. (1967). An onset-onset law for one case of apparent motion and metacontrast. *Perception & Psychophysics*, 2(12), 577–584.
- Khuu, S. K., Kidd, J. C., & Errington, J. A. (2010). The effect of motion adaptation on the position of elements in the visual saltation illusion. *Journal of Vision*, 10(12):19, 1–14, <http://www.journalofvision.org/content/10/12/19>, doi:10.1167/10.12.19. [PubMed] [Article]
- Khuu, S. K., Phu, J., & Khambiye, S. (2010). Apparent motion distorts the shape of a stimulus briefly presented along the motion path. *Journal of Vision*, 10(13):15, 1–15, <http://www.journalofvision.org/content/10/13/15>, doi:10.1167/10.13.15. [PubMed] [Article]
- Kolers, P. A. (1963a). A difference between real and apparent visual movement. *Nature*, 197, 271–272.
- Kolers, P. A. (1963b). Some differences between real and apparent visual movement. *Vision Research*, 61, 191–206.
- Kolers, P. A., & von Grunau, M. (1975). Visual construction of color is digital. *Science*, 187(4178), 757–759.
- Kolers, P. A., & von Grunau, M. (1976). Shape and color in apparent motion. *Vision Research*, 16(4), 329–335.
- Landis, C. (1954). Determinants of the critical flicker-fusion threshold. *Physiological Reviews*, 34(2), 259–286.
- Larsen, A., Madsen, K. H., Lund, T. E., & Bundesen, C. (2006). Images of illusory motion in primary visual cortex. *Journal of Cognitive Neuroscience*, 18(7), 1174–1180.
- Legge, G. E., & Foley, J. M. (1980). Contrast masking in human vision. *Journal of the Optical Society of America*, 70(12), 1458–1471.
- Lewis, D., & Khuu, S. (2010). Quantifying the perception of colour in visual saltation. *Journal of Vision*, 10(7): 435a, <http://www.journalofvision.org/content/10/7/435>, doi:10.1167/10.7.435. [PubMed]
- Liu, T., Slotnick, S. D., & Yantis, S. (2004). Human MT+ mediates perceptual filling-in during apparent motion. *Neuroimage*, 21(4), 1772–1780.
- Luria, S. M. (1965). Effects of continuously and discontinuously moving stimuli on the luminance threshold of a stationary stimulus. *Journal of the Optical Society of America*, 55(4), 418–425.
- Maeda, K., Yamamoto, H., Fukunaga, M., Umeda, M., Tanaka, C., & Ejima, Y. (2010). Neural correlates of color-selective metacontrast in human

- early retinotopic areas. *Journal of Neurophysiology*, 104(4), 2291–2301.
- Mikami, A., Newsome, W. T., & Wurtz, R. H. (1986). Motion selectivity in macaque visual cortex. II. Spatiotemporal range of directional interactions in MT and V1. *Journal of Neurophysiology*, 55(6), 1328–1339.
- Motoyoshi, I. (2007). Temporal freezing of visual features. *Current Biology*, 17(11), R404–406.
- Muckli, L., Kohler, A., Kriegeskorte, N., & Singer, W. (2005). Primary visual cortex activity along the apparent-motion trace reflects illusory perception. *PLoS Biology*, 3(8), e265.
- Nagai, T., Beer, R. D., Krizay, E. A., & Macleod, D. I. (2011). Spatiotemporal averaging of perceived brightness along an apparent motion trajectory. *Journal of Vision*, 11(7):5 1–15, <http://www.journalofvision.org/content/11/7/5>, doi:10.1167/11.7.5. [PubMed] [Article]
- Nagai, T., Kimura, H., & Nakauchi, S. (2011). Sensitivity impairment for detecting color alternation along an apparent motion trajectory. *Journal of Vision*, 11(11): 744, www.journalofvision.org/content/11/11/744, doi:10.1167/11.11.744. [Abstract]
- Neff, W. S. (1936). A critical investigation of the visual apprehension of movement. *The American Journal of Psychology*, 41(1), 1–42.
- Nishida, S., Watanabe, J., Kuriki, I., & Tokimoto, T. (2007). Human visual system integrates color signals along a motion trajectory. *Current Biology*, 17(4), 366–372.
- Otto, T. U., Ogmen, H., & Herzog, M. H. (2006). The flight path of the phoenix—the visible trace of invisible elements in human vision. *Journal of Vision*, 6(10):7, 1079–1086, <http://www.journalofvision.org/content/6/10/7>, doi:10.1167/6.10.7. [PubMed] [Article]
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, 10, 437–442.
- Pessoa, L., & De Weerd, P. (2003). *Filling-in: From perceptual completion to cortical reorganization*. New York: Oxford University Press, USA.
- Prins, N., & Kingdom, F. A. (2009). *Psychophysics: A Practical Introduction*. London, UK: Academic Press.
- Reeves, A. (1981). Metacontrast in hue substitution. *Vision Research*, 21(6), 907–912.
- Schwiedrzik, C. M., Alink, A., Kohler, A., Singer, W., & Muckli, L. (2007). A spatio-temporal interaction on the apparent motion trace. *Vision Research*, 47(28), 3424–3433.
- Shimozaki, S. S., Eckstein, M., & Thomas, J. P. (1999). The maintenance of apparent luminance of an object. *Journal of Experimental Psychology: Human Perception and Performance*, 25(5), 1433–1453.
- Squires, P. C. (1931). The influence of hue on apparent visual movement. *The American Journal of Psychology*, 43(1), 49–64.
- Sterzer, P., Haynes, J. D., & Rees, G. (2006). Primary visual cortex activation on the path of apparent motion is mediated by feedback from hMT+/V5. *Neuroimage*, 32(3), 1308–1316.
- Stoper, A. E., & Banffy, S. (1977). Relation of split apparent motion to metacontrast. *Journal of Experimental Psychology: Human Perception and Performance*, 3(2), 258–277.
- Verstraten, F. A., Cavanagh, P., & Labianca, A. T. (2000). Limits of attentive tracking reveal temporal properties of attention. *Vision Research*, 40(26), 3651–3664.
- von Grunau, M. W. (1978). Interaction between sustained and transient channels: form inhibits motion in the human visual system. *Vision Research*, 18(2), 197–201.
- Watanabe, J., & Nishida, S. (2007). Veridical perception of moving colors by trajectory integration of input signals. *Journal of Vision*, 7(11):3, 1–16, <http://www.journalofvision.org/content/7/11/3>, doi:10.1167/7.11.3. [PubMed] [Article]
- Watson, A. B., & Ahumada, A. J., Jr. (1985). Model of human visual-motion sensing. *Journal of the Optical Society of America A. Optics and Image Science*, 2(2), 322–341.
- Watson, A. B., & Pelli, D. G. (1983). QUEST: a Bayesian adaptive psychometric method. *Perception & Psychophysics*, 33(2), 113–120.
- Weisstein, N., & Growney, R. (1969). Apparent movement and metacontrast: A note on Kahneman's formulation. *Perception and Psychophysics*, 5(6), 321–328.
- Wertheimer, M. (1912). Experimentelle studien über das sehen von bewegung. *Zeitschrift für Psychologie*, 61, 161–265.
- Wibral, M., Bledowski, C., Kohler, A., Singer, W., & Muckli, L. (2009). The timing of feedback to early visual cortex in the perception of long-range apparent motion. *Cerebral Cortex*, 19(7), 1567–1582.
- Yantis, S., & Nakama, T. (1998). Visual interactions in the path of apparent motion. *Nature Neuroscience*, 1(6), 508–512.