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Dissociating Higher and Lower Order Visual Motion Systems by Priming Illusory Apparent Motion

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Abstract

Motion processing is thought of as a hierarchical system composed of higher and lower order components. Past research has shown that these components can be dissociated using motion priming paradigms in which the lower order system produces negative priming while the higher order system produces positive priming. By manipulating various stimulus parameters, researchers have probed these two systems using bistable test stimuli that permit only two motion interpretations. Here we employ maximally ambiguous test stimuli composed of randomly refreshing pixels in a task that allows observers to report more than just two types of motion percepts. We show that even with such stimuli, motion priming can constrain the unstructured random pixel patterns into coherent percepts of positive or negative apparent motion. Moreover, we find that the higher order system is uniquely susceptible to cognitive influences, as evidenced by a significant suppression of positive priming in the presence of alternative response options.

Keywords

apparent motion, motion aftereffects, priming, attention, higher order motion, lower order motion, top-down effects, multistable stimuli

Introduction

Higher and Lower Order Motion Processing

Over the last several decades, motion perception researchers have converged on a view of motion processing as a multilevel system composed of lower and higher order neural mechanisms (Britten, Shadlen, Newsome, & Movshon, 1992). The lower order components are understood as arrays of neurons instantiating spatiotemporal filters that detect motion energy, a measure of the correlation between luminance levels in space over time (Adelson & Bergen, 1985; Reichardt, 1957; Van Santen & Sperling, 1984). This system produces a

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directional signal when there is an unambiguous correspondence between luminance-defined features and can encode global motion patterns even in the absence of well-defined spatial structures (although a *counterchange model* may better capture correspondences when spatial structure is well-defined; see Norman, Hock, & Schöner, 2014). This is commonly referred to as first-order motion. When more complex relations define a stimulus, higher order mechanisms are employed to detect the presence of motion and to determine its character. Past studies have identified mechanisms that resolve motion in ambiguous, multistable stimuli or that solve correspondence problems between features determined by stimulus texture or depth-defined regions, known as second-order features (Anstis & Ramachandran, 1987; Jiang, Pantle, & Mark, 1998; Lu & Sperling, 1995a, 1995b, 1996, 2002; Pinkus & Pantle, 1997; Ramachandran & Anstis, 1983, 1985). Unlike simple motion energy detectors, higher order mechanisms, such as attentional feature tracking, can be intentionally manipulated to dissociate the two systems (Cavanagh, 1992; Culham & Cavanagh, 1994; Culham, Verstraten, Ashida, & Cavanagh, 2000; Verstraten, Cavanagh, & Labianca, 2000). This openness to top-down cognitive influence is characteristic of the higher order system.

The higher and lower systems also differ in how they are tuned for various stimulus factors (i.e., bottom-up influences), responding differently to contrast, motion velocity, frame rate, and the duration of the motion stimulus. Critically, the two systems respond to priming in opposite ways relative to these stimulus factors (Culham et al., 2000; Kanai & Verstraten, 2005; Pantle, Gallogly, & Piehler, 2000; Takeuchi, Tuladhar, & Yoshimoto, 2011; Wexler, Glennerster, Cavanagh, Ito, & Seno, 2013; Yoshimoto, Uchia-Ota, & Takeuchi, 2014). The lower order system produces motion percepts opposite the primed direction (i.e., negative priming, or motion aftereffects), and the higher order system produces motion percepts congruent with the primed direction. Our present study explores whether this dissociation between the lower and higher order systems can be achieved in the context of a maximally ambiguous stimulus that can be interpreted in more than just two ways.

Positive and Negative Priming in Bistable Dynamic Stimuli

The effect of motion adaptation is ancient knowledge: On the first page of his 1911 treaties, Wohlgemuth (1911) quotes Aristotle that, after observing flowing water, "objects at rest then seem to be in motion." The classic motion aftereffect is an illusory motion percept elicited when a static stimulus appears to move in the opposite (negative) direction of a moving adapter (or prime). Contemporary researchers consider this effect as a type of negative priming that has been explored in both static and dynamic, or flickering test stimuli (Bex, Verstraten, & Mareschal, 1996; Nishida & Ashida, 2000). In studies using dynamic test stimuli, participants are primed with an unambiguous motion signal and then tested with an ambiguous sequence of frames that can be resolved into one of two mutually exclusive directions. Using such dynamic test stimuli, researchers have identified not only negative priming but also instances of *positive priming*, in which the test stimuli appear to move in the same direction as a motion prime (Culham et al., 2000; Kanai & Verstraten, 2005; Nishida & Sato, 1992, 1995; Takeuchi et al., 2011; Yoshimoto et al., 2014). Most importantly, these studies have identified specific stimulus parameters that determine whether the induced illusory motion will be judged positive or negative with respect to the prime. For example, Kanai and Verstraten (2005) showed that the duration of the motion prime, as well as the duration of the interval between prime and test (inter-stimulus interval, or ISI), largely determines the directionality of illusory motion. Generally, longer prime durations lead to negative priming, whereas shorter prime durations lead to positive

priming. However, depending on the length of the ISI, the directionality of the illusory percepts can flip.

Takeuchi et al. (2011) and Yoshimoto et al. (2014) identified additional stimulus parameters that determine the directionality of motion priming. Takeuchi et al. (2011) showed that higher velocity stimuli and longer prime durations typically result in negative priming, whereas lower velocity stimuli and shorter prime durations lead to positive priming. The authors take this as evidence that the higher order motion system (which is thought to be insensitive to high-velocity motion) is responsible for the positive priming effects. They further showed that positive priming is facilitated in bright or photopic conditions, consistent with higher order feature tracking that benefits from high-contrast stimuli (Culham & Cavanagh, 1994). Following these findings, Yoshimoto et al. (2014) further showed that negative priming manifests only in retinotopic coordinates, whereas positive priming manifests in both retinotopic and spatiotopic coordinates. This is consistent with the functional magnetic resonance imaging (fMRI) evidence that V1 (i.e., lower order system) is tuned to retinotopic coordinates, and hMT+ (i.e., higher order system) is also tuned to spatiotopic coordinates (Crespi, Biagi, d'Avossa, Burr, Tosetti, & Morrone, 2011; d'Avossa, Tosetti, Crespi, Biagi, Burr, & Morrone, 2007).

We note that similar dissociative effects of positive and negative priming have been reported in nonmotion domains. For example, Long, Toppino, and Mondin (1992) showed that short preexposures to a nonambiguous Necker cube led participants to a congruent interpretation of a subsequently presented ambiguous Necker cube (analogous to positive priming), whereas long preexposures led to opposite interpretations (analogous to negative priming). Similarly, in the context of binocular rivalry, short and long preexposures can lead to facilitation or suppression of a rivalry stimulus, respectively (Brascamp, Knapen, Kanai, Van Ee, & Van Den Berg, 2007). Thus, the dissociative effects of positive and negative priming may reflect general low- and high-order mechanisms that resolve ambiguities across perceptual domains, while preserving similar temporal dynamics.

Positive, Negative, and Other Effects of Priming in Maximally Ambiguous Dynamic Stimuli

The studies we discussed earlier used test stimuli composed of first-order features (i.e., counter-phasing luminance-defined gratings) or second-order features (i.e., texture and depth) intended to produce *bistable* motion percepts. In these cases, priming served to bias observers to resolve the bistable test stimuli as one of two mutually exclusive motion interpretations. Even when using classic random dot cinematograms, which are multistable stimuli composed of hundreds or thousands of smoothly moving dots in random directions, participants are typically instructed to report one of only two motion directions, although anecdotally subjects have reported additional motion percepts in some studies (see Blake & Hiris, 1993; Davidenko, Heller, Cheong, & Smith, 2017; Hsieh & Tse, 2006). This leaves open the question: Do positive and negative priming effects account for all possible illusory motion percepts in a maximally ambiguous test stimulus that allows for a greater space of possible motion interpretations?

Other researchers have shown that when observing sufficiently complex apparent motion stimuli, a range of illusory motion patterns can be perceived (Blake & Hiris, 1993; Hsieh & Tse, 2006; Verstraten et al., 2000; Wertheimer, 1912). Even relatively simple multistable stimuli, such as a plus sign alternating with an X, can be resolved in at least three ways, including clockwise (CW) rotation, counterclockwise (CCW) rotation, and alternating CW and CCW motion (Verstraten et al., 2000; Wertheimer, 1912). As for more complex apparent

motion stimuli, such as those based on refreshing frames of random dots, an even larger set of global motion percepts have been described, including translational (or drifting), rotational, rebounding, contracting or expanding, and shearing motion (Blake & Hiris, 1993; Davidenko et al., 2017; Hsieh & Tse, 2006). Furthermore, we have preliminary evidence that even more complex motion patterns (such as multistep, or multidirectional motion) can be primed in sufficiently ambiguous stimuli, but that perceiving these motion patterns depends importantly on how attention is deployed. Despite the known range of possible motion percepts, past priming studies that relied on unidirectional priming stimuli used paradigms that could only measure unidirectional illusory motion percepts.

In our previous work, we used unidirectional (drifting) as well as bidirectional (rebounding) apparent motion primes in a persistence paradigm in which participants were primed with an apparent motion pattern and indicated when that pattern changed or stopped during a subsequent sequence of uncorrelated random dots (i.e., maximally ambiguous test stimuli; see Davidenko et al., 2017). We found that participants consistently perceived both illusory drifting and illusory rebounding motion consistent with the motion prime for many subsequent random frames, a phenomenon we termed illusory apparent motion (or IAM). Although it may seem parsimonious to interpret drifting IAM as a case of positive priming driven by the higher order attention-based motion system, there were several aspects of our paradigm that call for more direct confirmation of this interpretation. First, drifting IAM was elicited in the same paradigm as rebounding IAM, a more complex type of priming in which the primed motion pattern spans a larger temporal window, in this case involving two discrete motion steps. This effect had not been previously measured in the context of negative and positive priming, and thus, its association with positive priming has not been established. Second, obtaining both drifting and rebounding IAM in the same paradigm required presenting motion stimuli at a particularly slow, discrete frame rates (i.e., long frame durations), compared with previous work that relied on relatively smooth motion stimuli (i.e., short frame durations; see Blake & Hiris, 1993; Kanai & Verstraten, 2005; Takeuchi et al., 2011; Yoshimoto et al., 2014). Finally, participants in our persistence study often reported that the drifting IAM induced by a unidirectional drifting prime would sometimes break down into rebounding percepts, a phenomenon that has not been reported in studies of positive and negative priming. Thus, while it may seem that drifting IAM is the same phenomenon as positive priming, it is worth testing this claim directly under more controlled conditions.

The goals of the current study are twofold: First, we aim to establish that drifting IAM behaves just like positive priming by emulating previous studies that showed that manipulating relevant stimulus parameters in the prime can cause the priming direction to reverse. In Experiment 1, we manipulate the velocity of the priming motion, and in Experiment 2, we further manipulate frame duration and prime duration. Second, we aim to show that classic two-alternative forced choice (2AFC) tasks that only allow participants to report positive or negative motion fail to capture the wider range of illusory percepts that can arise from unidirectional priming. Therefore, we designed our experiments with a between-subjects manipulation in which half of our participants were given the option to report "something else" besides the two primed motion directions (i.e., a 3AFC task).

Methods and Results

Experiment 1: The Effect of Stimulus Velocity on IAM

Although we have studied drifting IAM in the context of a persistence task (see Davidenko et al., 2017), we decided to adopt a new task for the present studies. While a persistence task

is well suited to assess the strength of positive priming, it is not ideally suited to distinguish positive from negative priming. Therefore, we adapted a motion priming and classification task similar to those used in the past (Kanai & Verstraten, 2005; Takeuchi et al., 2011; Yoshimoto et al., 2014).

Participants. Participants were 39 undergraduate students at the University of California, Santa Cruz (UCSC), who gave informed consent and participated in exchange for course credit. The study was approved by UCSC's Institutional Review Board. On the basis of performance on catch trials (see Procedure), we eliminated nine participants for failing to correctly identify the motion direction on at least 70% of catch trials. Our results retained the same pattern with or without including these outliers.

Stimuli. Frames of apparent motion stimuli were constructed and presented using MATLAB. Each frame consisted of a random pixel array, with each pixel's brightness being sampled uniformly between white and black. The array was blurred using a low-pass filter with a two-pixel radius, and an annulus mask was applied giving each stimulus the appearance of a donut, with a fixation dot positioned at the center of the annulus. Participants were instructed to sit still, with their eyes approximately 18 in. away from the display screen, which had a refresh rate of 60 Hz. At this distance, the diameter of the outer ring of the annulus spanned approximately 12.0° of visual angle, and the inner ring spanned approximately 4.5°. CW and CCW global motion percepts were induced via motion capture by superimposing a low-frequency radial sine-wave grating on each new random pixel frame, thus imputing an unambiguous apparent motion signal to the underlying array of random pixels (Ramachandran & Cavanagh, 1987; see Figure 1).

In order to test the effect of priming velocity in Experiment 1, priming duration was held constant at 5 s, with a test phase that lasted for 2 s. The radial sine-wave grating rotated by a constant amount at 22.5° between successive frames, and we manipulated the priming velocity (operationalized as degrees around the annulus per second) by varying the frame duration (0.0625, 0.125, 0.25, 0.5, and 1 s) resulting in priming velocities of 360°, 180°, 90°, 45°, and 22.5° per second, respectively. We note that in order to keep the duration of the prime and test phases constant across these conditions, the total number of priming frames covaried with frame duration (i.e., 80, 40, 20, 10, or 5 priming frames, respectively; see Table 1). Although we chose to describe our stimulus manipulation in terms of velocity, prime duration, and frame duration, the same manipulations could be described in other terms (e.g., jump size, number of priming frames, and frame duration). We made our choice of the three factors for readability and to conform to the existing literature.

Procedure. Throughout the priming phase, the contrast of the sine-wave grating decreased by 20% every second, such that it disappeared the moment the test phase began. The test phase consisted entirely of randomly refreshing arrays of blurred pixels. During the priming phase, the fixation dot was black, differentiating it from the test phase, during which the fixation dot became white. Participants were instructed in each trial to fixate on the black dot at the center while paying attention to the global motion pattern defined by the sine-wave gratings, and then to report the direction of motion they perceived after the dot became white (i.e., during the random frames). In a between-subjects manipulation, half of the participants were instructed to respond either with two choices (2AFC task: CW or CCW), and the other half were instructed to respond with three choices (3AFC: CW, CCW, or "something else"; see Figure 1). Each experiment included 20 "catch trials" in which the sine-wave grating remained visible at 20% contrast throughout the test phase to confirm that

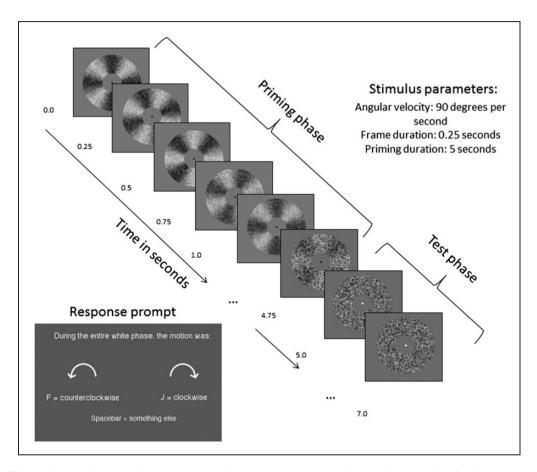


Figure 1. A schematic of the experimental stimuli and procedure. Arrays of randomly refreshing pixels superimposed on rotating sine gratings produce a priming motion pattern. Stimulus parameters are shown on the upper right. Participants were instructed to fixate on the central dot while attending to the global motion pattern. They were then asked to report the direction of motion perceived during the test phase, after the sine grating had faded away. The response prompt for the 2AFC was identical to that in the 3AFC task (shown on the bottom left) except that the "something else" option was not available.

Table 1. The Stimulus Parameters Manipulated in Experiments 1 and 2.

Stimulus parameters	Experiment I					Experiment 2a			Experiment 2b		
Angular velocity (deg/s)	360	130	90	45	22.5	45	45	45	45	45	45
Frame duration (s)	0.0625	0.125	0.25	0.5	I	0.125	0.25	0.5	0.125	0.25	0.5
Prime duration (s)	5	5	5	5	5	5	5	5	1.25	2.5	5
Number of priming frames	30	40	20	10	5	40	20	10	10	10	10
Degrees shifted per frame	22.5	22.5	22.5	22.5	22.5	5.625	11.25	22.5	5.625	11.25	22.5

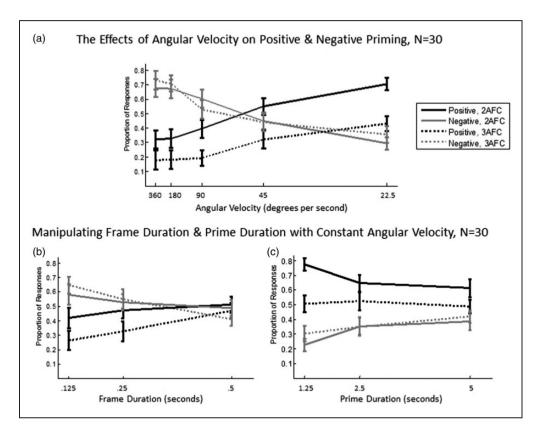


Figure 2. Average proportion of positive and negative priming. (a) In Experiment I, we manipulated *angular velocity*; solid lines represent the proportion of positive (black) and negative (gray) responses, in the 2AFC condition. Dotted lines represent responses in the 3AFC condition. (b) In Experiment 2a, we manipulated *frame duration* while holding angular velocity constant. (c) In Experiment 2b, we manipulated *prime duration* along with frame duration. Error bars represent the standard error of the mean across subjects.

participants were following the instructions. There were a total of 100 noncatch trials (5 Priming Velocities \times 2 Directions \times 10 Repetitions). The experiment lasted approximately 15 min.

Results. Figure 2(a) shows the proportion of trials in which positive (black) and negative (gray) priming effects were reported for each priming velocity. The solid lines, representing responses in the 2AFC condition, show a systematic increase in the proportion of positive priming as angular velocity decreases from 360° (0.32) to 22.5° per second (0.71), with a complementary decrease in negative priming.

The dotted lines show the proportion of positive (black) and negative (gray) priming in the 3AFC condition where participants also had a "something else" option. Here the proportion of negative priming remains relatively unaffected, while the proportion of positive priming is suppressed across all priming velocities, with significant suppression at 90° , 45° , and 22.5° per second (two-sample ts > 2.43; ps < .022). One possible explanation for the suppression of positive priming is that although motion percepts driven by the lower order system result from a mechanistic competition between adapted and nonadapted neural populations, percepts driven by higher order attention-based system are subject to more

interpretative mechanisms. That is, percepts driven by the higher order system may carry a degree of uncertainty or may explicitly represent motion percepts that do not fall strictly into the categories of CW or CCW motion. Despite the suppression of positive priming effects observed in the 3AFC task, the similar pattern of results across the two tasks demonstrates that positive and negative priming can both be induced in a maximally ambiguous stimulus by manipulating the angular velocity of the motion prime.

Experiment 2: Manipulating Frame Duration and Prime Duration With Constant Velocity

We note that in Experiment 1, angular velocity was conflated with both frame duration and number of priming frames; that is, high angular velocities were associated with short frame durations and large number of priming frames. Therefore, we cannot be sure which of these factors is driving the observed patterns of positive and negative priming. To tease these factors apart, Experiment 2a measures the effect of frame duration while holding angular velocity and prime duration constant. Experiment 2b measures the effect of prime duration while holding angular velocity and number of priming frames constant (see Table 1).

Participants. Participants were 41 undergraduate students at the UCSC who gave informed consent and participated in exchange for course credit. The study was approved by UCSC's Institutional Review Board. We eliminated 11 participants based on the same criterion as in Experiment 1, and again our results retained the same pattern with or without including these outliers.

Stimuli. We dissociated the effects of frame duration from stimulus velocity by varying how much the sine-wave grating shifted between successive frames. We tested three frame durations: For frame durations of 0.5 s, the grating shifted 22.5° (yielding a baseline condition consistent with Experiment 1); for frame durations of 0.25 s, it shifted 11.25°; and for frame durations of 0.25 s, it shifted 5.625° (see Table 1). Thus, in Experiment 2, the angular velocity of the priming motion was held constant at 45° per second. In Experiment 2a, the prime duration was kept constant at 5 s by varying the number of priming frames with the three frame durations (i.e., 40, 20, or 10 priming frames). In Experiment 2b, the number of priming frames was held constant at 10, thus producing three different prime durations, 1.25, 2.5, and 5 s.

Procedure. The structure of each trial was the same as in Experiment 1, and participants completed both Experiments 2a and 2b in separate blocks, with the order of blocks counterbalanced across participants. Each block included 10 catch trials and 60 noncatch trials (3 Frame Durations × 2 Directions × 10 Repetitions). The same between-subjects manipulation was carried out in between-subjects manipulation (i.e., half of the participants completed a 2AFC task and the other half a 3AFC).

Results. Figure 2(b) shows the effect of frame duration on the proportion of positive and negative priming when angular velocity and prime duration are held constant (Experiment 2a). Although a similar pattern of results is observed, in which positive priming increases with increasing frame durations, this effect is attenuated compared with Experiment 1. We can conclude from this that both velocity and frame duration contribute to the direction of motion priming. Considering the 3AFC condition in Figure 2(b), we again find that the introduction of a "something else" response option suppresses positive priming only.

This supports our argument that being able to report uncertainty or alternate motion percepts manifests primarily in the higher order motion system.

Figure 2(c) shows a slight decrease in positive priming effects as the prime duration increases from 1.25 to 5s (Experiment 2b). This decrease in positive priming is consistent with past research showing that the higher order system is more responsive to brief stimulus presentations. We note that the negative effect of prime duration overrides the positive effect of frame duration, which is also increasing from 0.125 to 0.5s in these stimuli. Once again, as in Experiments 1 and 2a, we found that the presence of a "something else" option suppresses positive priming responses and leaves negative priming responses intact.

Linear Regression Model

To characterize the relative contribution of the presence of "something else," angular velocity, frame duration, and prime duration on the average proportion of positive priming across participants, we defined a linear regression model as follows:

$$Y_{Pos} = c_{SE} \times X_{SE} + c_{Vel} \times X_{Vel} + c_{FD} \times X_{FD} + c_{PD} \times X_{PD}$$

where Y_{Pos} is the proportion of positive priming, X_{SE} is a categorical variable denoting the presence of a "something else" response option, X_{Vel} is the angular velocity, X_{FD} is the frame duration, and X_{PD} is the prime duration. The model is, thus, based on 22 data points: 10 from Experiment 1 (5 from the 2AFC task and 5 from the 3AFC task) and 12 from Experiment 2 (6 from 2AFC and 6 from 3AFC). The solution for this regression model results in the following (unscaled) coefficients, with significant coefficients shown in bold:

- $c_{SE} = -0.082$ (95% confidence interval [CI]: -0.112 to -0.052)
- $c_{Vel} = -0.00034$ (95% CI: -0.00074 to 0.00006)
- $c_{FD} = 0.28$ (95% CI: 0.13 to 0.43)
- $c_{PD} = -0.075$ (95% CI: -0.10 to -0.047)

The results indicate that (a) the presence of "something else" significantly reduced positive priming, (b) longer frame durations significantly increased positive priming, and (c) longer prime durations significantly decreased positive priming. In addition, the angular velocity of the priming motion had a marginal (p = .09) negative effect on positive priming. The full regression model accounts for 86% of the variability of positive priming responses across the experiments (see Figure 3).

As we noted, the inclusion of a "something else" option suppressed the proportion of positive priming while leaving the proportion of negative priming intact. The effect of the "something else" factor was not only significant for positive priming (mean difference between the proportion of positive priming for 2AFC vs. 3AFC: 0.164, 95% CI: 0.106–0.223; $t_{10} = 6.24$, p < .0001) and nonsignificant for negative priming (mean difference: 0.007, 95% CI: -0.260 to 0.041; $t_{10} = 0.50$, p > .5), but there was also a significant difference between the two effects ($t_{10} = 4.33$, p = .0015).

Discussion

Our studies were designed to address two goals: (a) to determine whether illusory percepts elicited in drifting IAM paradigms exist on a continuum between positive and negative priming and (2) to investigate whether the inclusion of a "something else" response

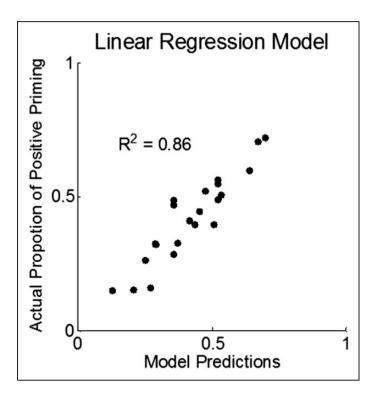


Figure 3. Linear regression model. The x-axis represents the predicted proportion of positive priming based on a linear model with four factors: (a) the presence of a "something else" response option, (b) angular velocity, (c) frame duration, and (d) prime duration. The y-axis represents the actual average proportion of positive priming responses across the 22 conditions in the 2AFC and 3AFC studies.

option can capture illusory percepts that are missed in classic 2AFC tasks. We addressed our first goal by showing that drifting IAM indeed exists on a continuum between positive and negative priming and is subject to the same dissociative priming effects of the higher and lower order motion processing systems as simpler, bistable stimuli used in the past (Culham et al., 2000; Kanai & Verstraten, 2005; Takeuchi et al., 2011; Yoshimoto et al., 2014). In Experiment 1, we found that higher angular velocities in the priming stimulus led to more negative priming, and lower velocities led to more positive priming. In Experiment 2a, we showed that longer frame durations led to more positive priming, and in Experiment 2b, we showed that longer prime durations led to more negative priming. When taken together in a linear regression model, we found that velocity and priming duration were negative predictors of positive priming, while frame duration was a positive predictor. While the effects of prime duration and angular velocity reflect what has been shown in previous work, our finding that longer frame durations (when isolated from stimulus velocity) are associated with more positive priming has not been previously described. One possibility for this finding is that during longer frames, the attentional system has a greater opportunity to solve the highly ambiguous correspondence problem, for example, by selecting visual features or pixel clusters to correspond with the previous or subsequent frame.

Our results addressed our second goal by showing that the presence of a "something else" response option in the 3AFC condition significantly reduced the proportion of positive priming while leaving negative priming intact. This result is consistent with our suspicion that unidirectional primes can indeed produce percepts other than positive or negative

priming. Furthermore, the surprising finding that introducing a "something else" option only affects percepts that would otherwise be classified as positive priming is consistent with the view that the higher order, attention-based motion system is more susceptible to cognitive influences than the lower order system.

What Is Happening When Participants Report Perceiving "Something Else"?

Based on our own observations and anecdotal reports by naïve participants, we believe there are three dominant types of percepts that elicit "something else" responses: (a) perceptually weaker instances of positive priming, (b) instances of positive priming that degrade into incoherence or reverse direction at some point during the test period, and (c) instances of positive priming that transform into other coherent motion percepts besides unidirectional CW or CCW motion.

The first type of percept can be explained in a relatively straightforward way: Compared with classic motion aftereffects (MAE) (negative priming), positive priming is simply less phenomenologically compelling as a motion percept (Pantle et al., 2000). It is possible that instances of positive priming are more variable in their appearance, at times appearing stronger or more coherent than at other times. A future study may prompt participants to provide confidence ratings or judgments of coherence as a way to directly assess whether positive priming percepts vary more in strength than negative priming percepts.

The second type of percept, in which positive priming degrades into incoherence or reverses its direction, can be accounted for by a more interesting, although still orthodox, explanation that stems from the dynamic competition between the higher and lower order systems. Specifically, depending on the degree to which the lower order system has adapted during the priming phase, it may override signals represented by the higher order system, such that over the duration of the test phase, initially positive motion percepts break down into one of two percepts: (a) incoherence (i.e., apparent randomness) if the two systems are near equilibrium or (b) a reversal of the motion direction (i.e., negative priming) if the lower order system is sufficiently adapted. Past studies provide evidence of this type of breakdown during a test phase, where, for example, positive priming reverts to negative priming (Nishida & Sato, 1992). A future study can investigate whether and when these breakdowns occur by manipulating the duration of the test phase: Shorter test phases should lead to "purer" instances of positive priming, whereas longer test phases should elicit higher rates of breakdown and an increase in "something else" responses.

The third and genuinely novel experience that participants may be classifying as "something else" are instances of positive priming that transform into other coherent motion patterns besides unidirectional CW or CCW motion. As we pointed out in the Introduction section, other researchers have reported a range of illusory motion percepts elicited by sufficiently complex multistable stimuli (Blake & Hiris, 1993; Hsieh & Tse, 2006; Verstraten et al., 2000; Wertheimer, 1912). Our own past work provides evidence that even in the absence of a priming stimulus, participants report spontaneous percepts of drifting and rebounding apparent motion when presented with random dot arrays refreshing at a sufficiently slow frame rate (i.e., with sufficiently long frame duration; see Davidenko, Cheong, & Smith, 2015). In fact, participants in those studies consistently showed a greater propensity to spontaneously report rebounding motion than drifting motion in such displays, suggesting that rebounding motion may be a "default" type of percept (see Hsieh & Tse, 2006; Verstraten et al. 2000). This idea is corroborated by anecdotal reports by participants from our persistence study (Davidenko et al., 2017) that IAM induced by unidirectional drifting primes would sometimes break down into rebounding motion.

A future study could characterize the different types of breakdown by asking participants to describe the percepts they experience during the test phase.

Do Changes in the Reporting Instructions Lead to Changes in the Distribution of Percepts?

It is possible that the alternative percepts described earlier (weak, incoherent, reversal, rebounding, or other coherent percepts) were experienced by participants in the 2AFC task just as often as in the 3AFC task, but that participants in the 2AFC task simply classified all of these percepts as positive priming. However, a more intriguing possibility is that the presence of the "something else" response option actually influenced the distribution of these percepts, leading participants in the 3AFC task to see more alternative percepts than participants in the 2AFC task. Namely, the mere expectation (i.e., high-level knowledge) that alternate motion patterns might exist within the test stimulus may have cued participants to selectively attend to motion signals they might have otherwise ignored. Such a mechanism would constitute a clear top-down effect, in which high-level knowledge modulates selective attention to promote one among many competing motion percepts. The fact that selective attention can modulate motion percepts is well-established (see Cavanagh, 1992; Culham & Cavanagh, 1994; Culham et al., 2000; Verstraten et al., 2000). Culham et al. (2000) even proposed the presence of "a cognitive process in which attention selects one among competing motion trajectories and suppresses the alternatives." Future studies can further explore the extent to which high-level knowledge (instructions, expectations, and intentions) can modulate visual attention and in turn create complex illusory motion patterns from pure noise.

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References

- Adelson, E. H., & Bergen, J. R. (1985). Spatiotemporal energy models for the perception of motion. Journal of the Optical Society of America A, 2, 284–299.
- Anstis, S., & Ramachandran, V. S. (1987). Visual inertia in apparent motion. *Vision Research*, 27, 755–764.
- Bex, P. J., Verstraten, F. A., & Mareschal, I. (1996). Temporal and spatial frequency tuning of the flicker motion aftereffect. *Vision Research*, *36*, 2721–2727.
- Blake, R., & Hiris, E. (1993). Another means for measuring the motion aftereffect. *Vision research*, 33, 1589–1592.
- Brascamp, J. W., Knapen, T. H., Kanai, R., Van Ee, R., & Van Den Berg, A. V. (2007). Flash suppression and flash facilitation in binocular rivalry. *Journal of Vision*, 7, 12–12.
- Britten, K. H., Shadlen, M. N., Newsome, W. T., & Movshon, J. A. (1992). The analysis of visual motion: A comparison of neuronal and psychophysical performance. *Journal of Neuroscience*, 12, 4745–4765.

- Cavanagh, P. (1992). Attention-based motion perception. Science, 257, 1563–1565.
- Crespi, S., Biagi, L., d'Avossa, G., Burr, D. C., Tosetti, M., & Morrone, M. C. (2011). Spatiotopic coding of BOLD signal in human visual cortex depends on spatial attention. *PLoS One*, 6, e21661.
- Culham, J. C., & Cavanagh, P. (1994). Motion capture of luminance stimuli by equiluminous color gratings and by attentive tracking. *Vision Research*, 34, 2701–2706.
- Culham, J. C., Verstraten, F. A., Ashida, H., & Cavanagh, P. (2000). Independent aftereffects of attention and motion. *Neuron*, 28, 607–615.
- Davidenko, N., Cheong, Y., & Smith, J. (2015). The suggestible nature of apparent motion perception. *Proceedings of the Cognitive Sciences Society*, July 2015.
- Davidenko, N., Heller, N. H., Cheong, Y., & Smith, J. (2017). Persistent illusory apparent motion in sequences of uncorrelated random dots. *Journal of Vision*, 17, 19, 1–17.
- d'Avossa, G., Tosetti, M., Crespi, S., Biagi, L., Burr, D. C., & Morrone, M. C. (2007). Spatiotopic selectivity of BOLD responses to visual motion in human area MT. *Nature Neuroscience*, 10, 249–255.
- Hsieh, P. J., & Tse, P. U. (2006). Stimulus factors affecting illusory rebound motion. *Vision research*, 46, 1924–1933.
- Jiang, Y., Pantle, A. J., & Mark, L. S. (1998). Visual inertia of rotating 3-D objects. Attention, Perception, & Psychophysics, 60, 275–286.
- Kanai, R., & Verstraten, F. A. (2005). Perceptual manifestations of fast neural plasticity: Motion priming, rapid motion aftereffect and perceptual sensitization. Vision Research, 45, 3109–3116.
- Long, G. M., Toppino, T. C., & Mondin, G. W. (1992). Prime time: Fatigue and set effects in the perception of reversible figures. Attention, Perception, & Psychophysics, 52, 609–616.
- Lu, Z. L., & Sperling, G. (1995a). The functional architecture of human visual motion perception. *Vision Research*, 35, 2697–2722.
- Lu, Z. L., & Sperling, G. (1995b). Attention-generated apparent motion. *Nature*, 377, 237–239.
- Lu, Z. L., & Sperling, G. (1996). Three systems for visual motion perception. *Current Directions in Psychological Science*, 5, 44–53.
- Lu, Z. L., & Sperling, G. (2002). Stereomotion is processed by the third-order motion system: Reply to comment on "Three-systems theory of human visual motion perception: review and update". *Journal of the Optical Society of America A*, 19, 2144–2153.
- Nishida, S. Y., & Ashida, H. (2000). A hierarchical structure of motion system revealed by interocular transfer of flicker motion aftereffects. *Vision Research*, 40, 265–278.
- Nishida, S. Y., & Sato, T. (1992). Positive motion after-effect induced by bandpass-filtered random-dot kinematograms. *Vision Research*, 32, 1635–1646.
- Nishida, S. Y., & Sato, T. (1995). Motion aftereffect with flickering test patterns reveals higher stages of motion processing. *Vision Research*, *35*, 477–490.
- Norman, J., Hock, H., & Schöner, G. (2014). Contrasting accounts of direction and shape perception in short-range motion: Counterchange compared with motion energy detection. *Attention, Perception, & Psychophysics*, 76, 1350–1370.
- Pantle, A. J., Gallogly, D. P., & Piehler, O. C. (2000). Direction biasing by brief apparent motion stimuli. Vision Research, 40, 1979–1991.
- Pinkus, A., & Pantle, A. (1997). Probing visual motion signals with a priming paradigm. *Vision Research*, 37, 541–552.
- Ramachandran, V. S., & Anstis, S. M. (1983). Extrapolation of motion path in human visual perception. *Vision Research*, 23, 83–85.
- Ramachandran, V. S., & Anstis, S. M. (1985). Perceptual organization in multistable apparent motion. Perception, 14, 135–143.
- Reichardt, W. (1957). Autokorrelations-auswertung als funktionsprinzip des zentralnervensystems. Zeitschrift für Naturforschung B, 12, 448–457.
- Takeuchi, T., Tuladhar, A., & Yoshimoto, S. (2011). The effect of retinal illuminance on visual motion priming. *Vision Research*, *51*, 1137–1145.

Van Santen, J. P., & Sperling, G. (1984). Temporal covariance model of human motion perception. Journal of the Optical Society of America A, 1, 451–473.

- Verstraten, F. A., Cavanagh, P., & Labianca, A. T. (2000). Limits of attentive tracking reveal temporal properties of attention. *Vision Research*, 40, 3651–3664.
- Wertheimer, M. (1912). Experimentelle Studium uber das Sehen von Bewegung. Zeitschrift fur Psychologie, 61, 161–265.
- Wexler, M., Glennerster, A., Cavanagh, P., Ito, H., & Seno, T. (2013). Default perception of high-speed motion. *Proceedings of the National Academy of Sciences*, 110, 7080–7085.
- Wohlgemuth, A. (1911). On the after-effect of seen movement. Vol. 1. Cambridge, England: University Press
- Yoshimoto, S., Uchida-Ota, M., & Takeuchi, T. (2014). The reference frame of visual motion priming depends on underlying motion mechanisms. *Journal of Vision*, 14, 10, 1–19.