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# Visual priming of two-step motion sequences

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Perception of an ambiguous apparent motion is influenced by the immediately preceding motion. In positive priming, when an observer is primed with a slow-pace (1–3 Hz) sequence of motion frames depicting unidirectional drift (e.g., Right–Right–Right–Right), subsequent sequences of ambiguous frames are often perceived to continue moving in the primed direction (illusory Right–Right ...). Furthermore, priming an observer with a slow-pace sequence of *rebounding* apparent motion frames that alternate between opponently coded motion directions (e.g., Right–Left–Right–Left) leads to an illusory continuation of the two-step rebounding sequence in subsequent random frames. Here, we show that even more arbitrary two-step motion sequences can be primed; in particular, two-step motion sequences that alternate between non-opponently coded directions (e.g., Up–Right–Up–Right; *staircase motion*) can be primed to be illusorily perceived in subsequent random frames. We found that staircase sequences, but not drifting or rebounding sequences, were primed more effectively with four priming frames compared with two priming frames, suggesting the importance of repeating the sequence element for priming arbitrary two-step motion sequences. Moreover, we compared the effectiveness of motion primes to that of symbolic primes (arrows) and found that motion primes were significantly more effective at producing prime-consistent responses. Although it has been proposed that excitatory and rivalry-like mechanisms account for drifting and rebounding motion priming, current motion processing models cannot account for our observed priming of staircase motion. We argue that higher order processes involving the recruitment and interaction of both attention and visual working memory are required to account for the type of two-step motion priming reported here.

## Introduction

It has long been known that an observer can perceive a static image as moving following the perception of veridical motion. As Aristotle noted that, after one observes flowing water, “objects at rest then seem to be in motion” (Wohlgemuth, 1911). This effect is a classic form of illusory motion known as the *motion aftereffect* (Hiris & Blake, 1992; Anstis, Verstraten, & Mather, 1998; Glasser, Tsui, Pack, & Tadin, 2011) and is also referred to as *negative motion priming*. More recently, researchers have shown that, if the static image is replaced with a sequence of ambiguous frames (such as flickering counterphase sine wave gratings), a stronger and longer lasting negative priming effect can be induced (Bex, Verstraten, & Mareschal, 1996; Nishida & Ashida, 2000). In such studies, participants are primed with a sequence of frames depicting unambiguous unidirectional motion (e.g., Right–Right–Right–Right) and then report that a sequence of subsequently viewed ambiguous frames, which can be resolved in one of two mutually exclusive directions, contains motion traveling opposite the primed direction (e.g., Left–Left–Left–Left). The basis of this reversal is believed to result from opponent coding observed in motion-sensitive neurons and constitutes a form of adaptation (Simoncelli & Heeger, 1998; Huk, Ress, & Heeger, 2001).

However, researchers have also identified a form of motion priming capable of overriding these opponent coding mechanisms (Ramachandran & Anstis, 1985; Nishida & Sato, 1992; Kanai & Verstraten, 2005). This effect has been referred to as *visual inertia* (Anstis & Ramachandran, 1987), *visual motion priming* (Pinkus & Pantle, 1997), and most recently *positive priming*

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(Takeuchi, Tuladhar, & Yoshimoto, 2011; Yoshimoto, Uchida-Ota, & Takeuchi, 2014), and it can bias the perception of subsequent ambiguous frames to be moving in the *same* direction as the priming frames. Specific stimulus parameters determine whether the induced illusory motion will be judged positive or negative relative to the priming frames. Such factors include prime duration, prime velocity, frame rate, length of the interstimulus interval (between the offset of priming frames and the onset of testing frames), and stimulus contrast (Kanai & Verstraten, 2005; Takeuchi et al., 2011; Yoshimoto et al., 2014; Heller & Davidenko, 2018).

There is evidence that the different percepts determined by stimulus parameters result from separate underlying mechanisms, one producing negative priming and the other producing positive priming (Pantle, Gallogly, & Piehler, 2000; Kanai & Verstraten, 2005; Yoshimoto et al., 2014; Heller & Davidenko, 2018; Yoshimoto & Takeuchi, 2019). Moreover, the evidence suggests that positive priming involves processes that are higher order than those responsible for negative priming. For example, Yoshimoto et al. (2014) showed that positive priming was predominantly reported in spatiotopic coordinates, implicating the role of frontal-parietal regions (Liu, Yu, Peter, & Cavanagh, 2019). In a later study Yoshimoto and Takeuchi (2019) found that directing attention away from the ambiguous test stimulus abolished the positive priming effect, strongly suggesting that attention is needed to induce positive priming. Recently, we showed that modulating participant's expectations about the range of possible motion sequences they might perceive influenced their reports of positive priming but failed to affect reports of negative priming (Heller & Davidenko, 2018). We also showed that instructions to hold (or change) a primed motion sequence lengthens (or shortens) the persistence of that motion sequence during the presentation of random frames (Allen, Jacobs, & Davidenko, 2022). Thus, it appears that higher order processes, including attention and expectation, are involved in positive priming in a way that they are not involved in negative priming. Although these findings suggest that priming is the output of more complex processes than motion aftereffects, the reliance on simple bistable stimuli has prevented an exploration of precisely how complex those processes are.

In this study, using *maximally ambiguous multistable* stimuli, we present novel evidence that positive priming can operate over more complex spatiotemporal motion sequences—in particular, two-step, staircase-like motion sequences (e.g., Up–Right–Up–Right). Here, we show that such staircase motion sequences can be primed similarly to simpler drifting (e.g., Up–Up–Up–Up) or rebounding (e.g., Up–Down–Up–Down) motion sequences (Davidenko, Heller, Cheong, & Smith, 2017; Davidenko & Heller, 2018). Furthermore,

we demonstrate that priming arbitrary two-step sequences is far more effective when the priming motion contains at least one repetition (i.e., two instances) of the sequence. Finally, we show that primes containing visual motion signals are more effective than symbolic primes (i.e., arrows). Our results suggest that visual working memory and selective attention must work together to produce the subsequent complex illusory percepts.

## Experiment 1: Priming drifting, rebounding, and staircase motion sequences

### Methods

In **Experiment 1**, we adapted a self-report paradigm we used previously to investigate the emergence of rebounding apparent motion following unidirectional (drifting) or bidirectional (rebounding) motion primes (Davidenko & Heller, 2018) (Figure 1). The present experiment was organized into three blocks in counterbalanced order that included (1) drifting primes, (2) rebounding primes, and (3) staircase primes. In each trial, we primed participants with five frames (i.e., an initial starting frame and four frame transitions) of random pixel arrays presented at a slow frame rate (1.5 Hz, or 667 ms per frame). This was equivalent to a motion velocity of 0.45°/s. The frame rate of 1.5 Hz was established in previous studies to lead to positive priming effects (Heller & Davidenko, 2018). The priming frames depicted two types of drifting motion (Up–Up–Up–Up or Down–Down–Down–Down), two types of rebounding motion (Up–Down–Up–Down or Down–Up–Down–Up), or two types of staircase motion (Up–Right–Up–Right or Down–Left–Down–Left). In target trials (80%), these priming frames were followed by two frames of uncorrelated random pixels, and participants were asked to report any directional motion they perceived in the two final frame transitions; in catch trials (20%), the two final frames contained real motion. Participants could press, in sequence, two of five buttons: four arrow buttons corresponding to the cardinal directions (Up, Down, Left, or Right) or a central asterisk button to indicate “Other” (either a different motion pattern or no coherent motion at all). This resulted in 25 possible response sequences (e.g., Up–Left, Down–Other). However, to avoid dependencies in the data, our analyses focus on directional response combinations only and exclude responses that included at least one Other button press (e.g., Up–Other, or Other–Other). Experiment and analysis scripts, as well as raw data files, can be accessed at <https://osf.io/nb8fj/>.

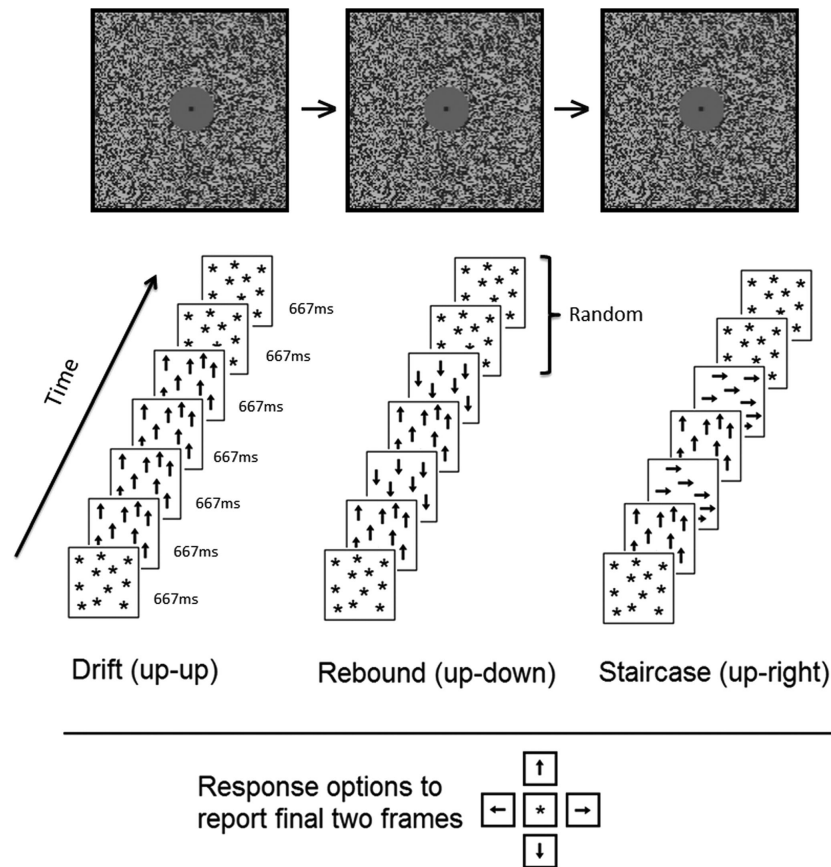


Figure 1. Example stimuli (top) and trial structure (bottom) for [Experiment 1](#). In each trial, observers were primed with five random pixel frames (an initial frame plus four frame transitions) depicting drifting (left), rebounding (middle), or staircase (right) motion. In experimental (non-catch) trials, the final two frames were completely random. Observers reported any motion perceived in the final two frames by making two sequential button presses depicting motion in one of the four cardinal directions or Other percept (asterisk).

## Participants

We recruited 23 undergraduate students (19 identifying as female, four as male; mean age, 19.7 years; range, 18–25) from 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 and took approximately 25 minutes to complete.

## Stimuli

Frames for the apparent motion stimuli were constructed and presented using MATLAB (MathWorks, Natick, MA) and Psychtoolbox 3. Each frame was composed of a  $140 \times 140$  array of random dark-gray or light-gray pixels. The center of the array was masked by a medium-gray circle with a 15-pixel radius, and a black fixation dot was positioned at the center of the mask ([Figure 1](#), top). The square array measured 6 inches on a side, and the circular mask

measured 1 inch in diameter; with a viewing distance of approximately 24 inches, the square array subtended  $14^\circ$  of visual angle, and the central mask subtended  $2.3^\circ$  of visual angle. In each trial, the priming motion consisted of five priming frames (an initial frame and four motion frame transitions) followed by two random test frames (two random frame transitions), with a fixed frame duration of 0.667 s. Translational motion was achieved by shifting a fixed random pixel array by 3 pixels in one of the cardinal directions, replacing the now missing rows or columns with new random pixels and randomizing the contrast polarity of 15% of the pixels of the array to add visual noise. Across three counterbalanced blocks, participants were primed with drifting motion (Up–Up–Up–Up or Down–Down–Down–Down), rebounding motion (Up–Down–Up–Down or Down–Up–Down–Up), or staircase motion (Up–Right–Up–Right or Down–Left–Down–Left) ([Figure 1](#), bottom). An example catch trial and an example experimental trial are shown in [Supplementary Movies S1 and S2](#), respectively.

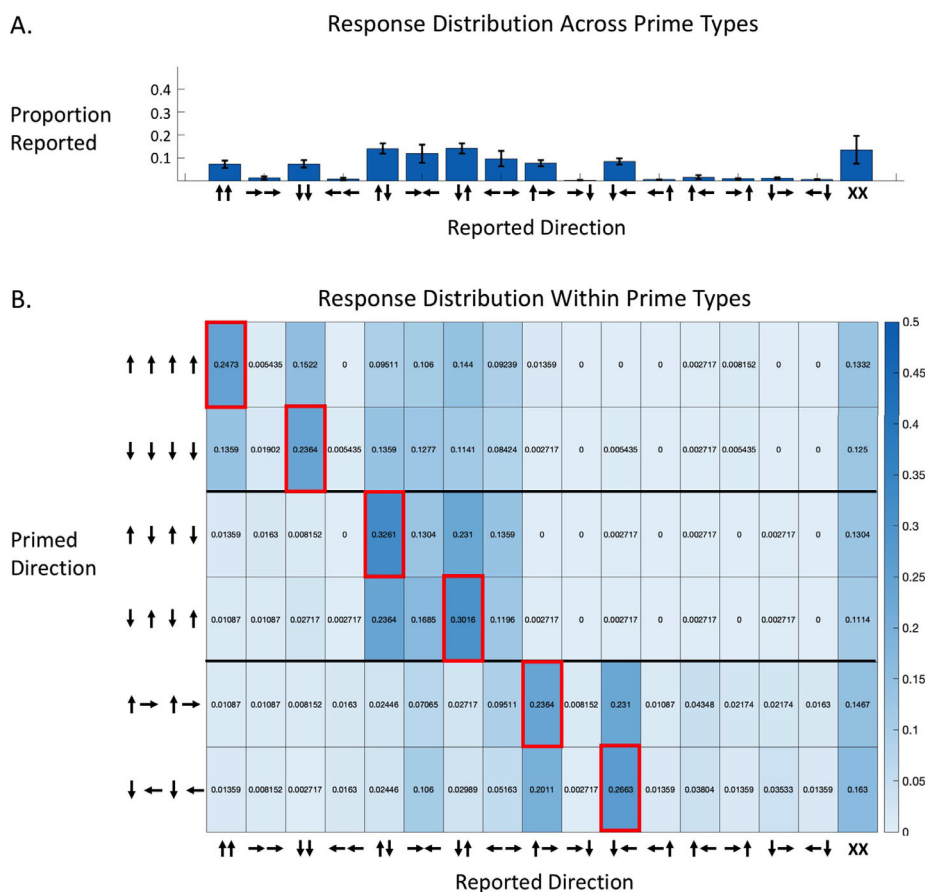


Figure 2. Results of Experiment 1. (A) The overall distribution of reported directions collapsed across all types of primes (drift, rebound, and staircase). Arrows along the x-axis indicate pairs of directions participants reported seeing in the last two random frames (e.g.,  $\uparrow\downarrow$  means the participant saw Up–Down). XX represents responses that included Other (e.g., Up–Other, Other–Other). Error bars represent a standard error of the mean across 23 participants. (B) The distribution of reported directions as a function of the primed motion. Arrows along the y-axis indicate the primed direction, and arrows along the x-axis represent reported directions, with XX indicating Other. Darker blue colors indicate higher proportions of responses, ranging from 0 to a maximum of 0.5. Cells highlighted by a red bounding box indicate prime-consistent responses.

**Procedure**

Participants were instructed to fixate on the fixation dot while attending to the global motion of the surrounding pixels and report what, if any, translational motion they perceived on the last two random frames by sequentially pressing two buttons with five options: Up, Left, Down, Right, or Other (where “Other” could represent any percept not captured by one of the first four options). This created a total of 25 possible response combinations in each trial; note that, for visualization, we grouped together all nine types of responses that included at least one Other button press (e.g., Up–Other, Other–Other), leaving 16 directional responses plus one combined Other response denoted as XX. Participants completed 32 trials in each motion sequence block. Within each block, the starting direction of the motion sequence (Up or Down) was randomized across trials. Before

each block, participants completed sets of 16 training trials in which the two final frames were not random but instead depicted a veridical motion sequence either consistent with or opposite the prime (e.g., Up–Up–Up–Up could be followed by Up–Up or Down–Down; Up–Right–Up–Right could be followed by Up–Right or Down–Left). Participants had to achieve performance of 70% or better on these training trials to move on to the main experiment. To ensure that participants were following instructions during the experiment, each block included eight catch trials that were similar to the training trials, with either consistent or inconsistent veridical motion on the final two frames.

**Results**

Figure 2 shows the response distribution for Experiment 1. Figure 2A (top) shows the overall

response distribution collapsed across all motion primes throughout the three blocks of the experiment. Note that some response types appear much more frequently than others; for example, the rebounding types of responses (e.g., Up–Down, Left–Right) are more frequent than others, which we have referred to in the past as the *rebounding bias* (Davidenko et al., 2017; Davidenko & Heller, 2018). A one-way repeated-measures analysis of variance (ANOVA) on the collapsed distribution of responses (excluding the combined denoting responses that included at least one Other button press responses) confirmed that the proportion of responses varied significantly by motion direction,  $F(15, 367) = 8.74, p < 0.0001$ . Figure 2B (bottom) shows this response distribution broken down by the preceding priming motion. The two top rows show the distribution of responses following drift primes, the next two rows following rebound primes, and the last two rows following staircase primes, as indicated by the arrows along the y-axis.

To investigate the effect of the priming motion on the reported motion directions, we conducted a two-way repeated-measures ANOVA on the proportion of responses, with one factor being the primed direction (six values) and the other factor being the reported direction (16 values, excluding combined XX responses). The results showed a significant main effect of reported direction,  $F(15, 2207) = 8.41, p < 0.0001$ , and a significant interaction between primed direction and reported direction,  $F(75, 2007) = 7.14, p < 0.0001$ . The main effect of reported direction reflects an overall propensity to report rebounding motion over other types of motion. Critically, the interaction indicates that the directions reported varied significantly as a function of the priming directions.

To test whether we successfully primed drift, rebound, and staircase motion sequences, we performed followup *t*-tests comparing the response rate for prime-consistent responses versus prime-inconsistent responses of the same type. Figure 3A shows the distribution of drift responses following drift primes. Note that the most frequent drift responses following drift primes matched the direction of the priming motion. Figure 3B directly compares the average proportion of prime-consistent ( $M = 0.242$ ) and prime-inconsistent ( $M = 0.053$ ) drift responses following drift primes. A paired *t*-test confirmed that prime-consistent responses were significantly more frequent,  $t(22) = 2.75; p = 0.005$ , one-tailed; Cohen's  $d = 0.57$ .

Similarly, Figure 3C shows the distribution of rebound responses following rebound primes. Following each type of rebound prime (e.g., Up–Down–Up–Down), the most frequent rebound responses were again consistent with the primed direction (e.g., Up–Down). Figure 3D compares the average proportion of

prime-consistent ( $M = 0.314$ ) and prime-inconsistent ( $M = 0.170$ ) rebound responses following rebound primes, revealing a significantly larger proportion of prime-consistent responses, paired  $t(22) = 2.75; p = 0.04$ , one-tailed; Cohen's  $d = 0.37$ .

Finally, Figures 3E and 3F show similar results for staircase primes. The average proportion of prime-consistent staircase responses ( $M = 0.251$ ) was significantly larger than prime-inconsistent staircase responses following staircase primes,  $M = 0.048$ ; paired  $t(22) = 3.22; p = 0.004$ , one-tailed; Cohen's  $d = 0.67$ . This constitutes evidence that two-step (i.e., staircase) motion sequences can be primed.

### Catch trial performance

Performance on catch trials was calculated as the proportion of correct two-button responses (e.g., pressing Up–Down when presented with veridical Up–Down motion on the final two frames). Based on 25 possible response combinations, chance-level performance was 0.04, and because each participant completed a total of 24 catch trials, the threshold for above-chance performance ( $p < 0.05$ ) was 0.1217. According to this criterion, all participants performed well above chance, with the lowest performance being 0.250 and the highest 1.00, with a mean of 0.750. Similar catch trial performance was observed in Experiments 2, 3, and 4, so we do not report the details of catch trial performance for those analyses.

### Summary discussion

Experiment 1 shows that staircase sequences can be primed similarly to how drifting and rebounding sequences have been primed in the past (Davidenko et al., 2017; Davidenko & Heller, 2018). However, it is possible that because we blocked trials by motion type and only presented two types of motion sequences for each type of motion, participants may have formed a global expectation that those specific motion sequences could be perceived and reported. This can be seen in the relatively high prevalence of those motion sequences within each block, even when they are not directly primed. For example, Down–Left responses ( $M = 0.231$ ) occurred nearly as frequently as Up–Right responses ( $M = 0.236$ ) following Up–Right–Up–Right primes. Because of the block design, it is difficult to distinguish whether these responses were directly primed by the preceding motion, or whether they were primed in a more global way as a result of seeing many such motion sequences across the experimental block. For example, during a staircase block, where every trial started with a staircase sequence (either Up–Right–Up–Right or Down–Left–Down–Left),

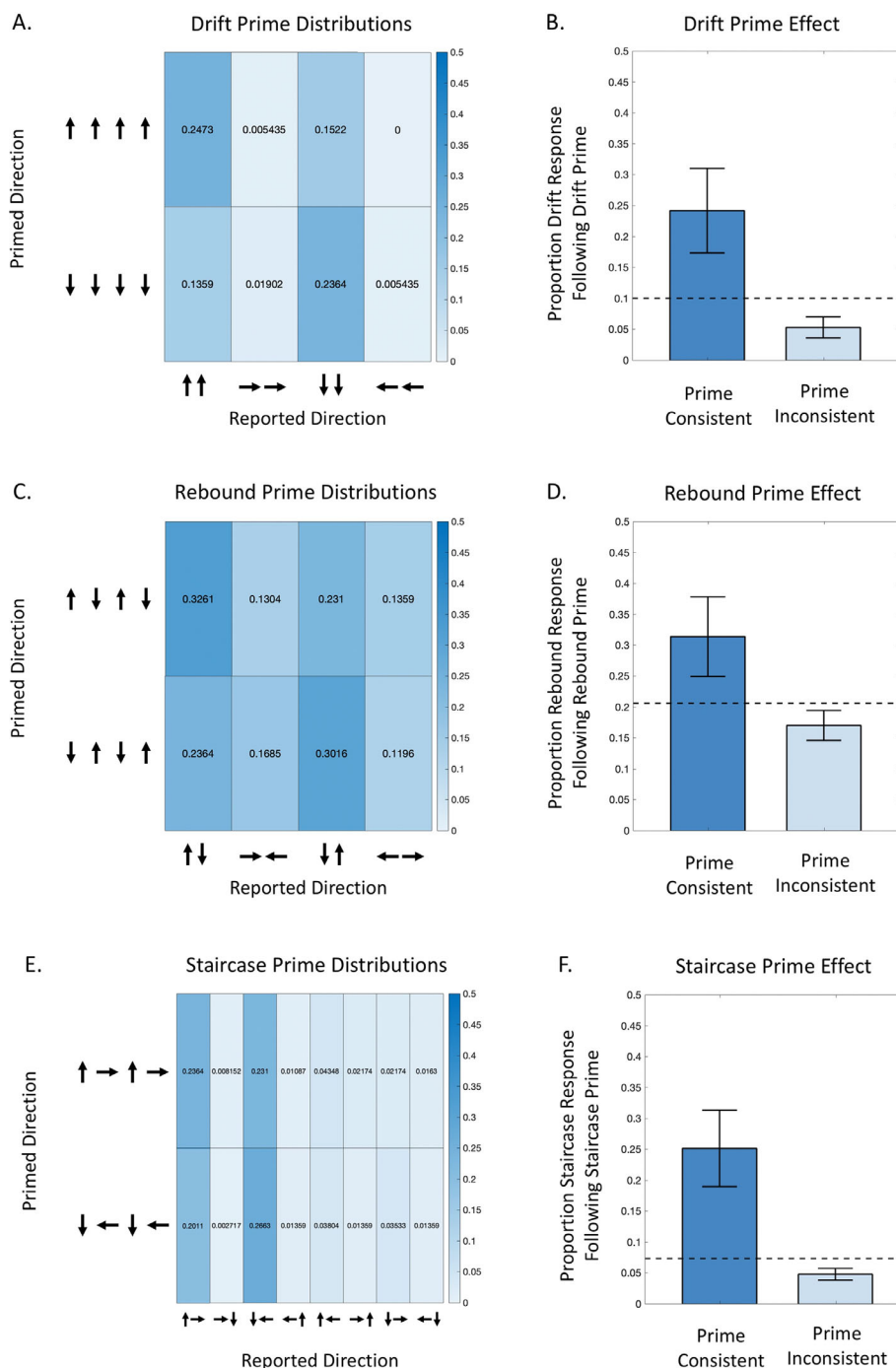


Figure 3. Results of Experiment 1 broken down by type of primed and reported directions (drift, A and B; rebound, C and D; staircase, E and F). (A) Distribution drift responses following drift primes. (B) Proportion of prime-consistent drift responses are shown in dark blue and prime-inconsistent drift responses in light blue (e.g., following a prime of ↑↑↑↑, a response of ↑↑ would be a prime-consistent drift response, and a response of ↓↓ would be a prime-inconsistent drift response). Error bars indicate a standard error of the mean across 23 participants. The dashed line indicates the average proportion of overall drift responses. (C) Distribution of rebound responses following rebound primes. (D) Proportion of prime-consistent and prime-inconsistent rebound responses. (E) Distribution of staircase responses following staircase primes. (F) Proportion of prime-consistent and prime-inconsistent staircase responses.

participants may have formed an expectation that those specific staircase sequences are frequent and to be expected, and it was this global expectation that influenced what they perceived and reported during the test frames.

Thus, the effects we found could be explained by two different mechanisms: (1) a global expectation in which specific staircase sequences are observed frequently, are learned throughout the time scale of the entire block, and influence what participants report; or (2) a more direct visual priming phenomenon where the immediately preceding motion (e.g., Up–Right–Up–Right) conditions the visual system such that subsequent ambiguous frames are interpreted consistent with that specific primed motion pattern (e.g., Up–Right). To distinguish between these two possibilities, we designed [Experiment 2](#) to reduce global expectations by first interspersing priming trials of all types (drift, rebound, and staircase) in equal proportions, rather than blocked by motion type. In addition, we included every type of motion sequence as a possible prime (16 possible combinations) rather than the six specific sequences selected in [Experiment 1](#). This was done to reduce participant bias to expect to see any particular motion sequence.

## Experiment 2: Priming drifting, rebounding, and staircase motion sequences in randomly interspersed trials

### Methods

[Experiment 2](#) was similar to [Experiment 1](#), except that trials with different motion primes (drifting, rebounding, and staircase) were randomly interspersed throughout the study rather than being blocked by motion type. In each trial, participants observed five frames (i.e., an initial starting frame and four frame transitions) of random pixel arrays presented at a slow frame rate (1.5 Hz, or 667 ms per frame) depicting one of the three motion types. Rather than restricting the motion sequences to specific motion directions (e.g., either Up–Up–Up–Up or Down–Down–Down–Down), all combinations of motion direction were possible. That is, the first two frames could display any sequence of motion directions (e.g., Right–Down, Left–Left, Up–Left), and the next two frames repeated the sequence. The only constraint we imposed was that the three types of motion sequence (drift, rebound, and staircase) occurred with the same frequency. Because there are twice as many unique motion sequences that would be classified as staircase motion (eight) than drift (four) or rebound (four), we downweighted the

probability of any particular staircase sequence by half, so that overall in the experiment there would be the same number of staircase, drifting, and rebounding trials.

As in [Experiment 1](#), during target trials (80%) the priming frames were followed by two frames of uncorrelated random pixels, and participants were asked to report any directional motion they perceived in the two final frame transitions. In catch trials (20%), the two final frames contained a real motion signal in any combination of the four cardinal directions. Participants were instructed to press, in sequence, two buttons: four cardinal direction arrow buttons (Up, Down, Left, or Right), or a central asterisk button to indicate Other (either a different motion pattern or no coherent motion at all). This resulted in 25 possible response sequences (e.g., Up–Left, Down–Other). For the analyses, we grouped together all nine responses that included Other and denoted them as XX.

### Participants

Compared with the blocked design of [Experiment 1](#), we expected that the interspersed trial design of [Experiment 2](#) would produce smaller priming effects overall. Assuming an effect size of about half as large as in [Experiment 1](#) (where Cohen's  $d$  in the staircase condition was 0.67), a power analysis with 80% power to detect an effect size of 0.33 with an alpha level of 0.05 would require a sample of about 67 participants. We recruited 68 undergraduate students (51 identifying as female, 15 as male; mean age, 20.1 years; range, 19–25) from UCSC, who gave informed consent and participated in exchange for course credit. The study was approved by UCSC's Institutional Review Board and took approximately 25 minutes to complete.

### Stimuli

Frames for the apparent motion stimuli were constructed and presented using MATLAB and Psychtoolbox 3 in a similar way as in [Experiment 1](#). Each frame was composed of a  $140 \times 140$  array of random dark-gray or light-gray pixels, the center of which was masked by a medium-gray circle with a 15-pixel radius, and a black fixation dot was positioned at the center of the mask. In each trial, the priming motion consisted of five priming frames (an initial frame and four motion frame transitions) followed by two random test frames (two random frame transitions), with a fixed frame duration of 0.667 s. Translational motion was achieved by shifting a fixed random pixel array by 3 pixels in one of the cardinal directions, replacing the now missing rows or columns with new random pixels, and randomizing the contrast polarity of 15% of the pixels of the array to add visual





Figure 4. Results of Experiment 2. (A) The overall distribution of reported directions collapsed across all primed directions. Arrows along the x-axis indicate pairs of directions participants reported seeing in the last two random frames (e.g.,  $\uparrow\downarrow$  means the participant saw Up–Down). XX represents responses that included Other (e.g., Up–Other, Other–Other). Error bars represent a standard error of the mean across 68 participants. (B) The distribution of reported directions as a function of the primed direction. Arrows along the y-axis indicate the primed direction, and arrows along the x-axis represent reported directions seen in the last two random frames. Darker blue colors indicate higher proportions of responses, ranging from 0 to a maximum of 0.5.

noise. In each trial, the first two frame transitions could depict any combination of cardinal directions, and the following two frame transitions repeated that combination. The probability of each motion sequence was weighted to ensure that the experiment included the same number of drifting, rebounding, and staircase trials.

### Procedure

The procedure was nearly identical to Experiment 1. Participants were instructed to fixate on the central dot while attending to the global motion of the surrounding pixels and report what, if any, translational motion they perceived on the last two random frames by sequentially pressing two buttons with five options: Up, Left, Down, Right, or Other (where “Other” could represent any percept not captured by one of the first four options). This created a total of 25 possible response combinations in each trial. In Experiment 2,

participants completed a total of 180 trials: 48 trials depicting each of the three motion types (drifting, rebounding, and staircase), plus 36 catch trials. Before beginning the experiment, participants completed sets of 16 training trials in which the two final frames were not random but instead depicted a veridical motion sequence (e.g., Up–Up–Up–Up could be followed by Right–Left, Down–Right, or any other combination). Participants needed to achieve performance of 70% or better on these training trials to move on to the main experiment. To ensure that participants were following instructions during the experiment, the main experiment included 36 catch trials that were similar to the training trials, with veridical motion on the final two frames.

### Results

Figure 4 shows the average distribution of responses across the 68 participants in Experiment 2. Figure 4A

shows the overall response distribution averaged across the entire experiment (i.e., collapsing across all motion primes). A one-way repeated-measures ANOVA on the collapsed distribution of responses (excluding the combined XX responses) confirmed that the proportion of responses varied significantly by motion direction,  $F(15, 1087) = 20.35$ ,  $p < 0.0001$ . Figure 4B shows this broken down by the 16 different motion prime conditions (the first four rows show drift primes, the next four rebound primes, and the next eight staircase primes). Darker blue colors on the matrix indicate more frequent responses. As can be seen, the diagonal elements representing prime-consistent responses have a darker blue color, indicating that prime-consistent motion sequences were frequently reported.

To investigate the effect of the priming motion on the reported motion directions, we conducted a two-way repeated-measures ANOVA on the proportion of responses, with one factor being the primed directions (16 values) and the other factor being the reported directions (16 values, excluding combined XX responses). The results showed a significant main effect of primed direction,  $F(15, 17,407) = 5.74$ ,  $p < 0.0001$ ; a significant main effect of reported direction,  $F(15, 17,407) = 15.9$ ,  $p < 0.0001$ ; and a significant interaction,  $F(225, 17,407) = 10.5$ ,  $p < 0.0001$ . The main effect of reported direction reflects an overall propensity to report rebounding motion over other types of motion. Critically, the interaction indicates that the directions reported varied as a function of the priming directions.

To test whether we successfully primed drifting, rebound, and staircase motion sequences, we performed followup  $t$ -tests comparing the frequency of prime-consistent responses versus prime-inconsistent responses of the same motion type. Figure 5A shows the distribution of drift responses following drift primes. The diagonal elements (which indicate prime-consistent responses) have a darker blue color than the rest of the cells. To quantify this, Figure 5B compares the average proportion of prime-consistent ( $M = 0.112$ ) and prime-inconsistent ( $M = 0.019$ ) drift responses following drift primes, showing a significantly larger proportion of prime-consistent responses, paired  $t(67) = 6.35$ ;  $p < 0.0001$ , one-tailed; Cohen's  $d = 0.77$ . Similarly, Figure 5C shows the distribution of rebound responses following rebound primes. Figure 5D compares the average proportion of prime-consistent ( $M = 0.179$ ) and prime-inconsistent ( $M = 0.075$ ) rebound responses following rebound primes, revealing a significantly larger proportion of prime-consistent responses, paired  $t(67) = 5.38$ ;  $p < 0.0001$ , one-tailed; Cohen's  $d = 0.65$ .

Figures 5E and 5F show similar results for staircase primes. The average proportion of prime-consistent staircase responses ( $M = 0.132$ ) was significantly

larger than that for prime-inconsistent staircase responses ( $M = 0.024$ ), paired  $t(67) = 7.83$ ;  $p < 0.0001$ , one-tailed; Cohen's  $d = 0.950$ . This again shows that arbitrary two-step motion sequences can be primed similarly to drifting and rebounding motion sequences.

## Summary discussion

The results of Experiment 2 suggest that perceptions of illusory staircase sequences are the result of a trial-by-trial priming effect, rather than high-level expectations that are built during a consistent exposure to a particular motion sequence in a block, as trials of different motion types were randomly interspersed throughout the experiment. It is worth noting, however, that the change between a blocked design in Experiment 1 and randomized trial design in Experiment 2 resulted in fewer prime-consistent responses overall. This suggests that the global context introduced by blocking trials by prime type in Experiment 1 had a positive effect on the likelihood of prime-consistent responses.

The successful priming of staircase motion sequences raises the question of what constitutes a motion sequence? In other words, how many motion frames are necessary to establish a motion sequence? For a drifting sequence, two motion frames (e.g., Up–Up) should be enough to indicate that it is a drifting motion sequence. For a rebounding sequence, it could be argued that four motion frames (e.g., Up–Down–Up–Down) are necessary to denote the repeating sequence; otherwise, Up–Down could be part of a more complex sequence, such as Up–Down–Right–Left–etc. However, as we have argued previously, even a single instance of Up–Down could tap into an intrinsic oscillatory mechanism between opponently coded motion detectors, resulting in the type of priming effects reported here and elsewhere (Hsieh, Caplovitz, & Tse, 2005; Davidenko & Heller 2018). We therefore predicted that a single instance of Up–Down (i.e., two priming frames) would be sufficient to prime rebounding motion.

For a staircase motion sequences, however, a single instance (e.g., Up–Right) does not necessarily denote a staircase sequence; for example, Up–Right could indicate the beginning of a rotational motion sequence such as Up–Right–Down–Left–etc. Furthermore, because staircase motion is composed of non-opponent motion directions, observing a single Up followed by Right should not tap into any intrinsic oscillatory mechanism like a rebounding (e.g., Up–Down) sequence does. Therefore, we predicted that two frames of staircase motion (e.g., Up–Right) would not be sufficient to prime staircase-consistent responses. Experiment 3 was designed to test this hypothesis.

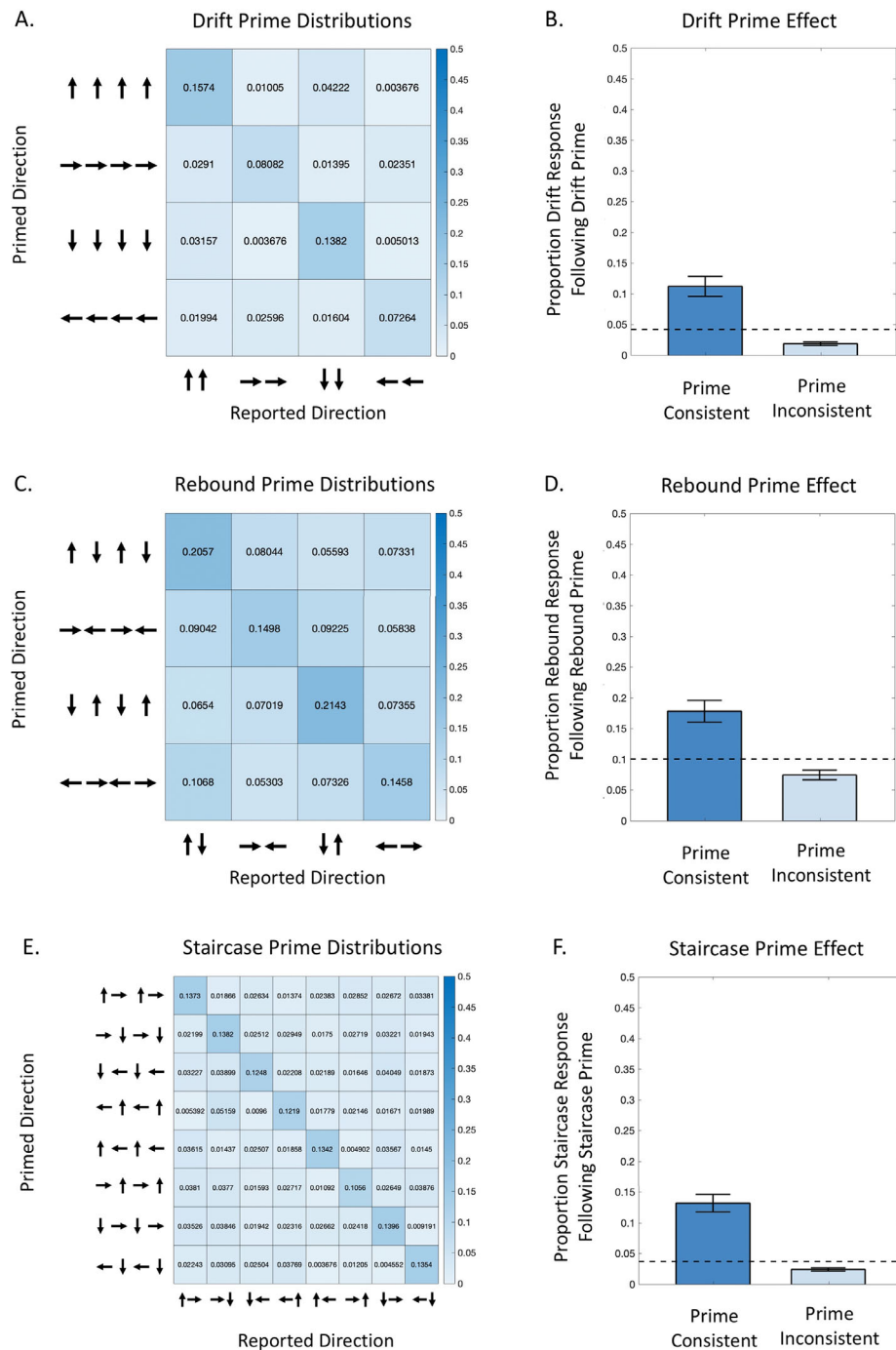


Figure 5. Results of Experiment 2 broken down by type of primed and reported directions (drift, A and B; rebound, C and D; staircase, E and F). (A) Distribution drift responses following drift primes. (B) Proportion of prime-consistent drift responses in dark blue and prime-inconsistent drift responses in light blue (e.g., following a prime of ↑↑↑↑, a response of ↑↑ would be a prime-consistent drift response and a response of ↓↓ would be a prime-inconsistent drift response). Error bars indicate a standard error of the mean across 68 participants. The dashed line indicates the average proportion of overall drift responses. (C) Distribution of rebound responses following rebound primes. (D) Proportion of prime-consistent and prime-inconsistent rebound responses. (E) Distribution of staircase responses following staircase primes. (F) Proportion of prime-consistent and prime-inconsistent staircase responses.

## Experiment 3: Priming drifting, rebounding, and staircase motion sequences in interspersed trials with only two priming frames

### Methods

**Experiment 3** was nearly identical to **Experiment 2**, except that in each trial participants observed only three frames (i.e., an initial starting frame and two frame transitions) of random pixel arrays presented at a slow frame rate (1.5 Hz, or 667 ms per frame) depicting one of the three motion types. Supplementary Movie S3 shows an example of an experimental trial from **Experiment 3**. The two priming frame transitions could depict any sequence of motion directions (e.g., Right–Down, Left–Left, Up–Left). The only constraint we imposed was that the three types of motion sequence (drift, rebound, and staircase) occurred with the same frequency, as in **Experiment 2**. In target trials (80%) the priming frames were followed by two frames of uncorrelated random pixels, and participants were asked to report any directional motion they perceived in the two final frame transitions. In catch trials (20%), the two final frames contained real motion in any combination of the cardinal directions. Participants were instructed to press, in sequence, two of five buttons: four cardinal direction arrow buttons (Up, Down, Left, or Right) or a central asterisk button to indicate “Other” (either a different motion pattern or no coherent motion at all). This resulted in 25 possible response sequences (e.g., Up–Left, Down–Other).

### Participants

We recruited 66 undergraduate students (48 identifying as female, 18 as male; mean age, 19.7 years; range, 19–24) from UCSC, who gave informed consent and participated in exchange for course credit. The study was approved by UCSC’s Institutional Review Board and took approximately 20 minutes to complete.

### Stimuli

Frames for the apparent motion stimuli were constructed and presented using MATLAB and Psychtoolbox 3 in a similar way as in **Experiment 2**, except that the priming motion consisted of only two priming frame transitions (an initial frame and two motion frame transitions). In each trial, the first two frame transitions could depict any combination of cardinal directions, and the following two frame

transitions either were completely random (regular trials) or depicted veridical motion (catch trials). As in **Experiment 2**, the probability of each motion sequence was weighted to ensure that the experiment included the same number of drifting, rebounding, and staircase priming trials.

### Procedure

The procedure was identical to that for **Experiment 2** except that the stimuli contained only two priming frames.

### Results

**Figure 6** shows the average distribution of responses across the 66 participants in **Experiment 2**. **Figure 6A** shows the overall response distribution averaged across the entire experiment (i.e., collapsing across all motion primes). A one-way repeated-measures ANOVA on the collapsed distribution of responses (excluding the combined XX responses) confirmed that the proportion of responses varied significantly by motion direction,  $F(15, 1055) = 12.85, p < 0.0001$ . **Figure 6B** shows this distribution broken down by the 16 different motion prime conditions (the first four rows show drift primes, the next four show rebound primes, and the next eight show staircase primes. Darker blue colors indicate more frequent responses. As can be seen, the diagonal elements representing prime-consistent responses have a darker blue color for drift and rebound motion primes, but this is not as clear for staircase primes.

To investigate the effect of the priming motion on the reported motion directions, we conducted a two-way repeated-measures ANOVA on the proportion of responses, with one factor being the primed directions (16 values) and the other factor being the reported directions (16 values, excluding combined XX responses). The results showed a significant main effect of reported direction,  $F(15, 16,895) = 14.26, p < 0.0001$ ; and a significant interaction between primed direction and reported direction,  $F(225, 16,895) = 8.84, p < 0.0001$ . The main effect of reported direction reflects an overall propensity to report rebounding motion over other types of motion. Critically, the interaction indicates that the directions reported varied significantly as a function of the priming motion.

To test whether two priming frames were sufficient to prime drifting, rebound, and staircase motion, we performed followup *t*-tests comparing the frequency of prime-consistent responses versus prime-inconsistent responses of the same type. **Figure 7A** shows the distribution of drift responses following drift primes. The diagonal elements (which indicate prime-consistent responses) have a darker blue color than the rest of

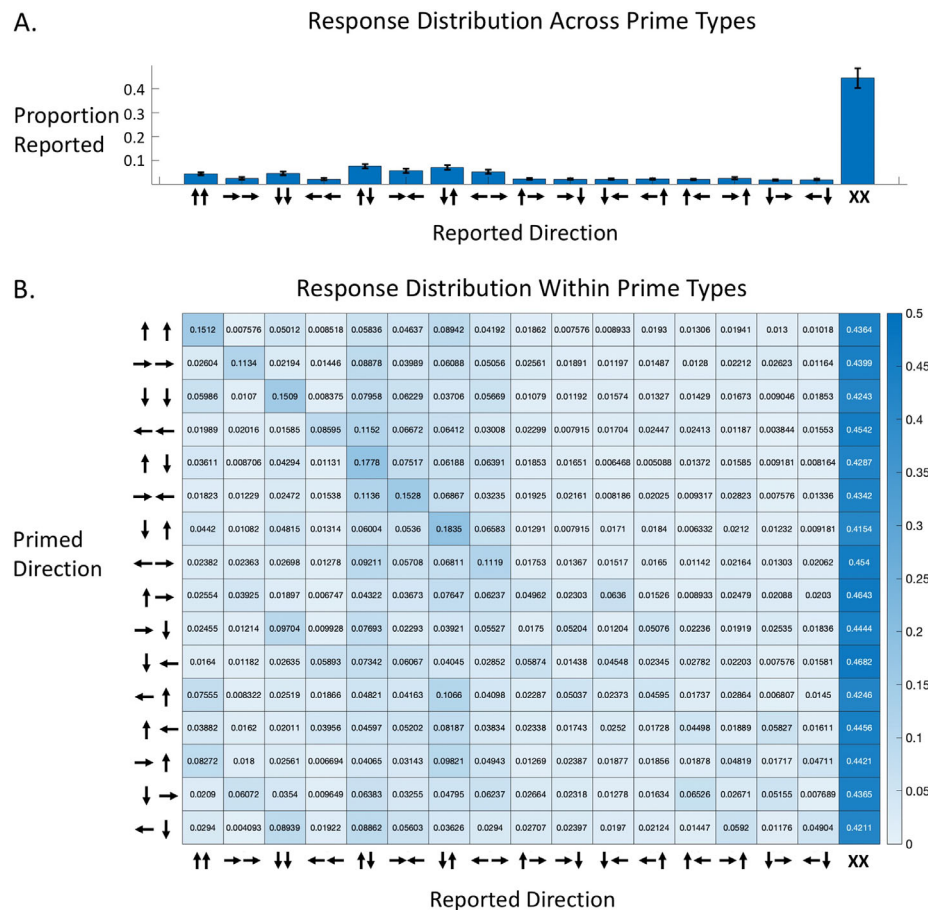


Figure 6. Results of Experiment 3. (A) The overall distribution of reported directions collapsed across all primed directions. Arrows along the x-axis indicate pairs of directions participants reported seeing in the last two random frames (e.g.,  $\uparrow\downarrow$  means the participant saw Up–Down). XX represents responses that included Other (e.g., Up–Other, Other–Other). Error bars represent a standard error of the mean across 66 participants. (B) The distribution of reported directions as a function of the primed direction. Arrows along the y-axis indicate the primed direction, and arrows along the x-axis represent reported directions seen in the last two random frames. Darker blue colors indicate higher proportions of responses, ranging from 0 to a maximum of 0.5.

the cells. To quantify this, Figure 7B compares the average proportion of prime-consistent ( $M = 0.126$ ) and prime-inconsistent ( $M = 0.022$ ) drift responses following drift primes, showing a significantly larger proportion of prime-consistent responses, paired  $t(65) = 5.08$ ;  $p < 0.0001$ , one-tailed; Cohen’s  $d = 0.63$ . Similarly, Figure 7C shows the distribution of rebound responses following rebound primes. Figure 7D compares the average proportion of prime-consistent ( $M = 0.155$ ) and prime-inconsistent ( $M = 0.067$ ) rebound responses following rebound primes, revealing a significantly larger proportion of prime-consistent responses, paired  $t(65) = 5.08$ ,  $p < 0.0001$ , one-tailed; Cohen’s  $d = 0.59$ .

Finally, Figures 7E and 7F show results for staircase primes. The average proportion of prime-consistent staircase responses ( $M = 0.047$ ) was significantly larger than prime-inconsistent staircase responses ( $M = 0.024$ ),  $t(65) = 2.87$ ;  $p = 0.006$ , one-tailed;

Cohen’s  $d = 0.35$ . Although this result suggests that it is possible to prime a staircase sequence with only two priming frames, the effect size and overall proportion of staircase-consistent responses were small.

### Comparing results between Experiments 2 and 3

Figure 8 shows a comparison of prime-consistent responses between Experiment 2 (with four priming frames) and Experiment 3 (with two priming frames). To test whether the number of priming frames (four or two) and the type of motion (drift, rebound, or staircase) affected responses, we conducted a two-way mixed-effects ANOVA, with the between-group factor being the number of priming frames (two levels) and the within-group factor being the motion type (three levels). The results revealed no main effect of

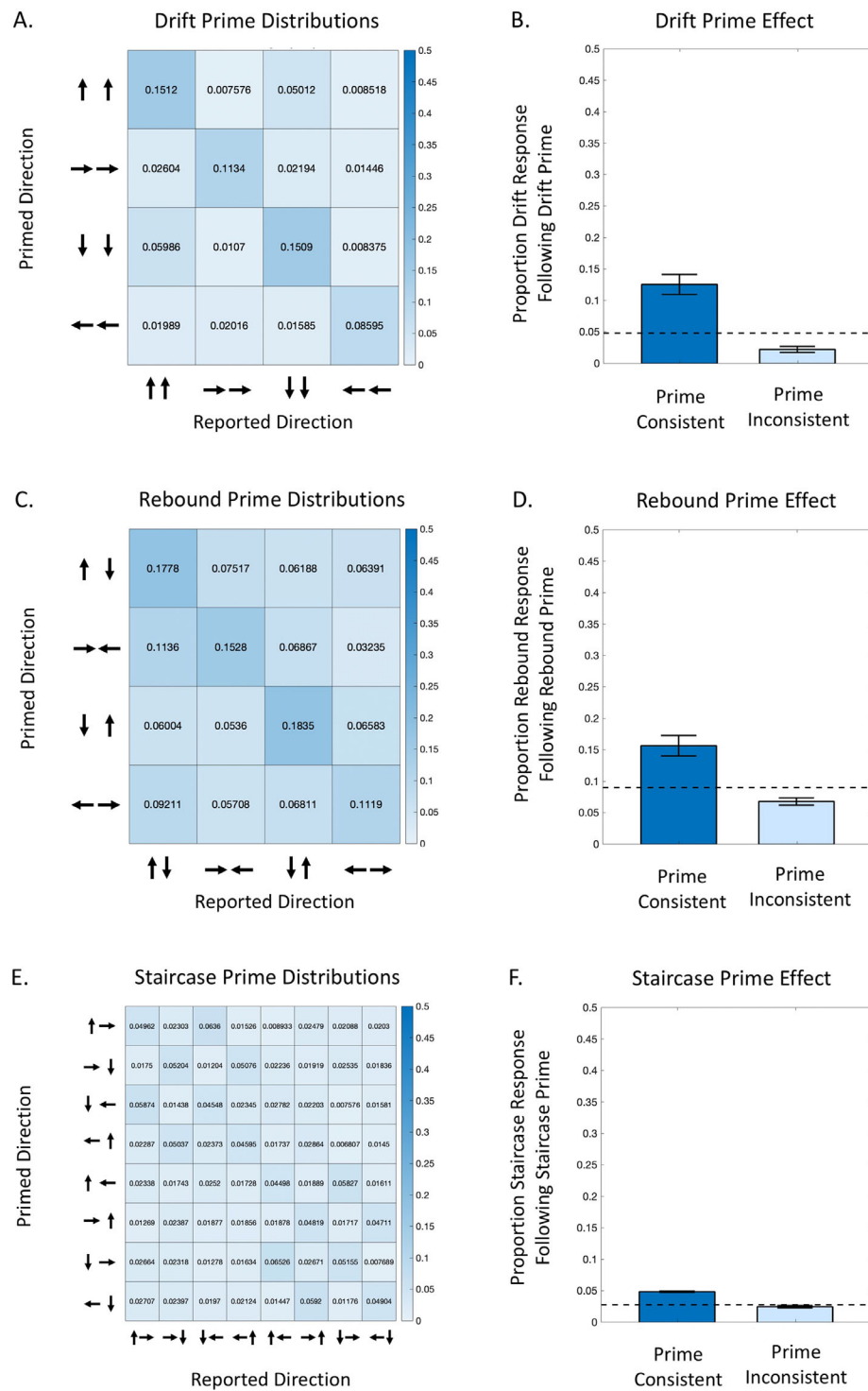


Figure 7. Results of Experiment 3 broken down by type of primed and reported directions (drift, A and B; rebound, C and D; staircase, E and F).

the number of priming frames but a significant main effect of the type of motion,  $F(15, 16,895) = 14.26$ ,  $p < 0.0001$ , reflecting that rebound motion responses occurred more frequently than other types of responses. Critically, there was also a significant interaction between the number of priming frames and the motion

type, such that prime-consistent staircase responses were significantly more frequent following four-frame primes ( $M = 0.1321$ ) compared with two-frame primes ( $M = 0.047$ ). A followup two-sample  $t$ -test confirmed that this difference was significant,  $t(132) = 5.16$ ;  $p < 0.0001$ , one-tailed; Cohen's  $d = 0.89$ .

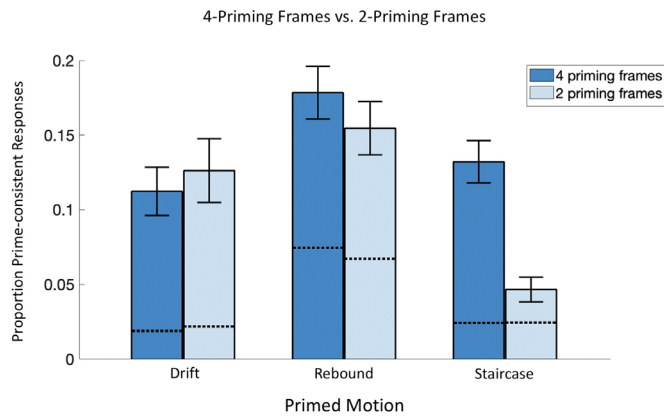


Figure 8. Comparison of prime-consistent responses across Experiments 2 and 3. Dark blue bars show results from Experiment 2 ( $n = 68$ ) with four priming frames (e.g.,  $\uparrow \rightarrow \uparrow \rightarrow$ ), and light blue bars show results from Experiment 3 ( $n = 66$ ) with two priming frames (e.g.,  $\uparrow \rightarrow$ ). Results are shown separately for drift, rebound, and staircase motion types. Dashed lines indicate the average proportion of prime-inconsistent responses for drift, rebound, and staircase motion primes in the two experiments. Error bars indicate a standard error of the mean across participants.

## Summary discussion

Being exposed to two priming frames or four priming frames was similarly effective at priming drift and rebound motion sequences, but for staircase sequences four priming frames were much more effective than two. These results suggest that priming arbitrary two-step motion sequences such as a staircase sequence is much more successful when participants are exposed to at least two iterations of the sequence elements (e.g., Up–Right–Up–Right) rather than just one iteration (Up–Right).

## Do these priming effects reflect a purely top–down process?

Although the results of the experiments above suggest that it was the motion stimulus that led to subsequent prime-consistent percepts, it is possible that similar priming effects can be accomplished without actual motion, using only symbolic primes. Anecdotally, we have seen that motion percepts can be primed simply with spoken words (e.g., saying Up, Down, Up, Down) (Davidenko et al., 2017). It is therefore possible that visual motion itself is not necessary to prime two-step motion percepts, but that a symbolic prime might produce similar results. Experiment 4 sought to test whether motion sequences (drift, rebound, and staircase) can be primed symbolically by the use of static arrows just like they can be primed with real motion.

## Experiment 4: Comparing visual and symbolic motion primes

### Methods

To test whether motion and arrow primes can produce similar results, we designed a replication and extension of Experiment 2, in which we observed robust evidence of two-step motion priming following four priming frames. Here, participants completed both a motion prime block (identical to Experiment 2) and a symbolic prime block in which participants saw a sequence of four static arrows that could point up, right, down, or left during the four priming frames, followed by two random pixel frames (see Stimuli).

### Participants

We recruited 67 undergraduate students (52 identifying as female, 13 as male, two as non-binary; mean age, 19.3 years; range, 18–22) from UCSC, who gave informed consent and participated in exchange for course credit. The study was approved by UCSC’s Institutional Review Board and took approximately 45 minutes to complete.

### Stimuli

The stimuli for the motion priming block were identical to those for Experiment 2. The stimuli for the arrow priming block presented a sequence of static arrows at the same presentation rate (1.5 Hz) at the center of a fixed random pixel frame. After the presentation of the fourth arrow, the arrow disappeared, and the pixel array changed randomly twice at 1.5 Hz (except during catch trials in which the two final frames showed coherent motion in any combination of the cardinal directions). Supplementary Movie S4 shows an example of an arrow priming trial from Experiment 4.

### Procedure

Participants completed both blocks, the order of which was counterbalanced across participants. As a result, 33 participants completed the motion priming block first, and 34 completed the arrow priming block first.

### Results

Figure 9 shows the average distribution of responses across the 67 participants in Experiment 4. Figure 9A

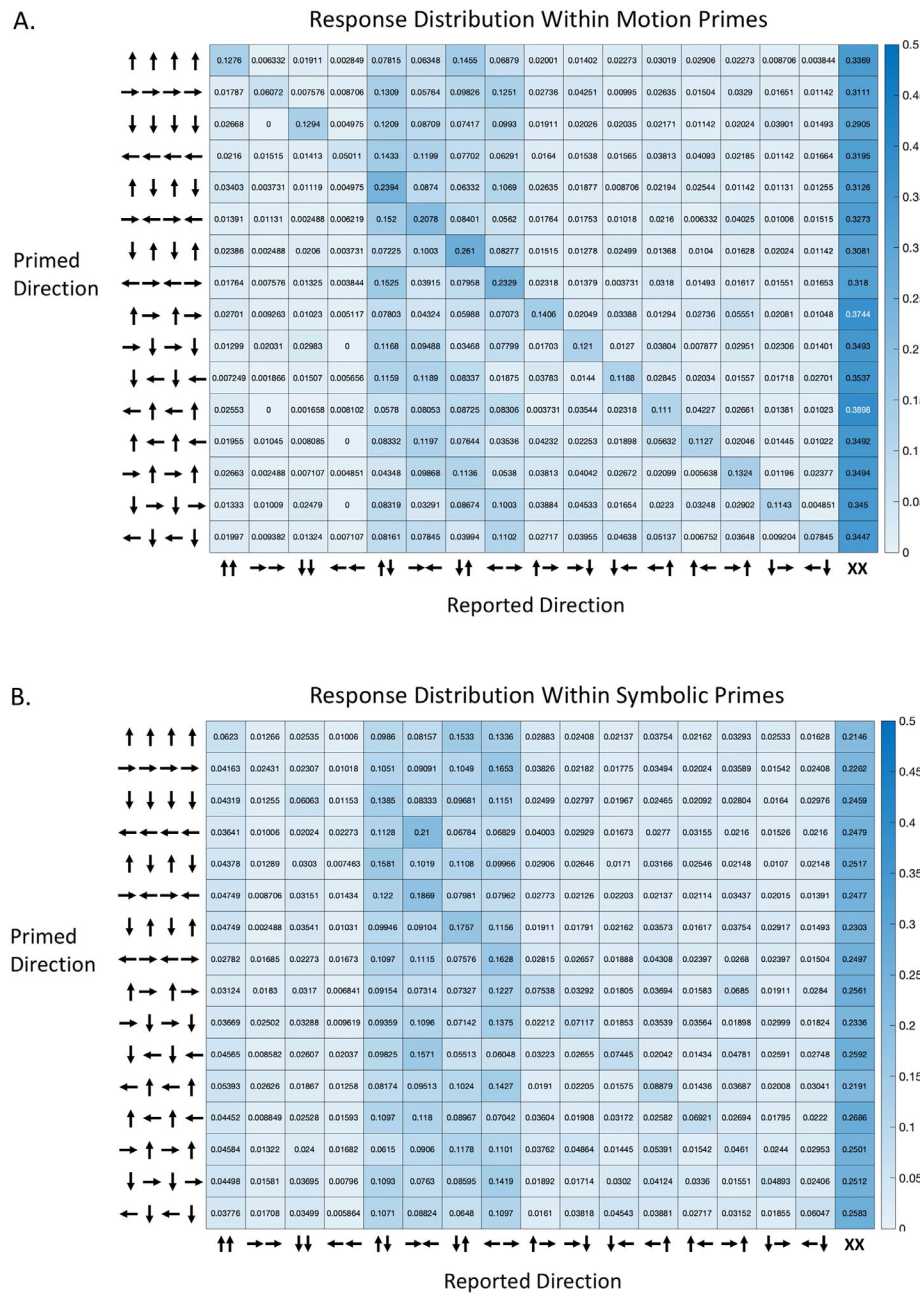


Figure 9. The distribution of average responses across participants for Experiment 4. The top panel shows the distribution of responses for motion primes, the bottom panel for arrow primes.

shows responses during the motion prime block, and Figure 9B shows responses during the arrow prime block. As can be seen, the diagonal elements representing prime-consistent responses have a darker blue color in the top panel compared with the bottom panel, suggesting that motion is more effective than arrows at priming subsequent motion percepts.

We conducted a three-way repeated-measures ANOVA with factors of priming type (motion or arrows), priming motion (16 levels), and reported motion (16 levels, excluding combined XX responses).

The results revealed a significant main effect of reported direction,  $F(15, 34,303) = 30.90$ , indicating a rebound bias and a significant main effect of prime type,  $F(1, 34,303) = 11.55$ ,  $p = 0.001$ , indicating significantly more cardinal direction motion responses following arrow primes. There was also a significant two-way interaction between prime direction and reported direction,  $F(225, 34,303) = 11.09$ ,  $p < 0.0001$ , indicating that the primed direction affected the reported direction. Critically, there was a significant three-way interaction among primed direction, reported direction, and



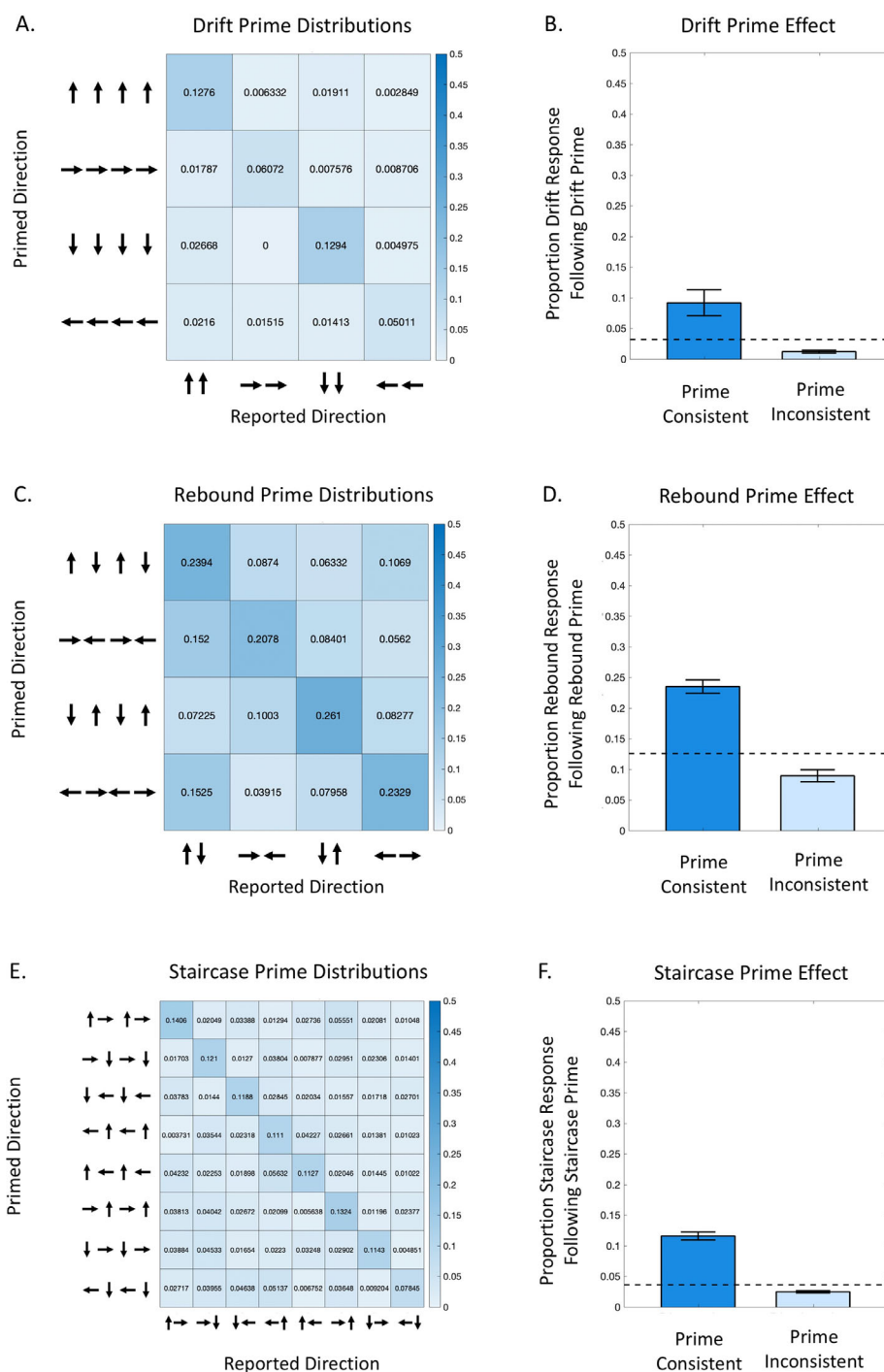


Figure 10. Results of the motion block from Experiment 4 broken down by type of primed and reported directions (drift, A and B; rebound, C and D; staircase, E and F).

prime type,  $F(225, 34,303) = 2.64, p < 0.0001$ . The three-way interaction indicated that motion primes were more effective than arrow primes at influencing the distribution of reported directions (see also Figure 12).

To test whether we successfully primed drifting, rebound, and staircase motion sequences, we performed followup *t*-tests comparing the response rate for prime-consistent responses versus prime-inconsistent

responses of the same type, separately for the motion prime block (Figure 10) and the arrow prime block (Figure 11). Figure 10A shows the distribution of drift responses following drift motion primes. The diagonal elements (which indicate prime-consistent responses) have a darker blue color than the other cells. To quantify this, Figure 10B compares the average proportion of prime-consistent ( $M = 0.092$ )

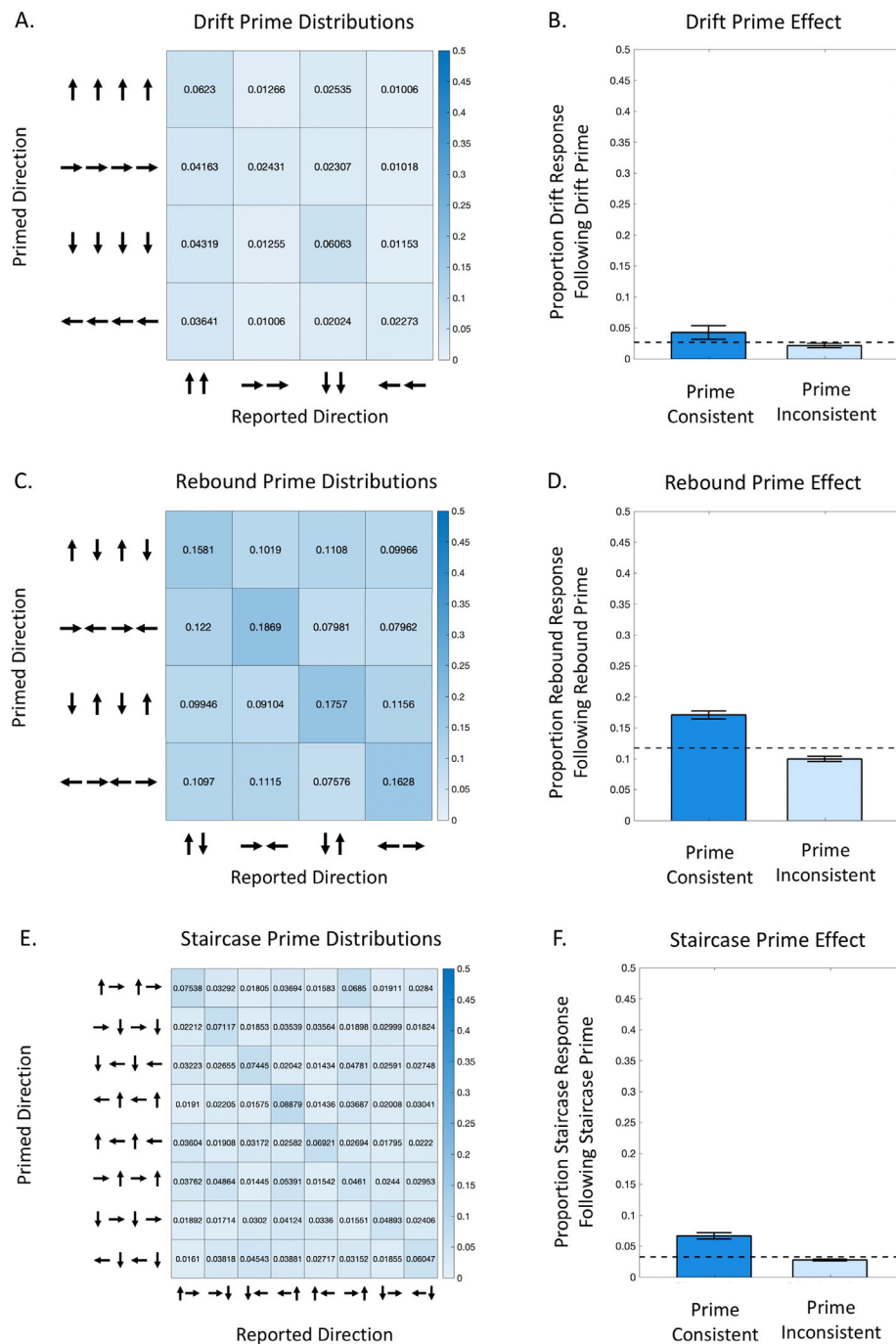


Figure 11. Results of the arrow block from Experiment 4 broken down by type of primed and reported directions (drift, A and B; rebound, C and D; staircase, E and F).

and prime-inconsistent ( $M = 0.012$ ) drift responses following drift primes, showing a significantly larger proportion of prime-consistent responses, paired  $t(66) = 4.61$ ;  $p < 0.0001$ , one-tailed; Cohen's  $d = 0.56$ . Similarly, Figure 10C shows the distribution of rebound responses following rebound primes in the motion prime block. Figure 10D compares the average proportion of prime-consistent ( $M = 0.2355$ ) and prime-inconsistent ( $M = 0.090$ ) rebound responses

following rebound primes, revealing a significantly larger proportion of prime-consistent responses, paired  $t(66) = 5.61$ ;  $p < 0.0001$ , one-tailed; Cohen's  $d = 0.69$ . Figures 10E and 10F show results for staircase primes. The average proportion of prime-consistent staircase responses ( $M = 0.117$ ) was significantly larger than prime-inconsistent staircase responses ( $M = 0.025$ ), paired  $t(65) = 6.37$ ;  $p < 0.0001$ , one-tailed; Cohen's  $d = 0.78$ . Overall, the results of the motion

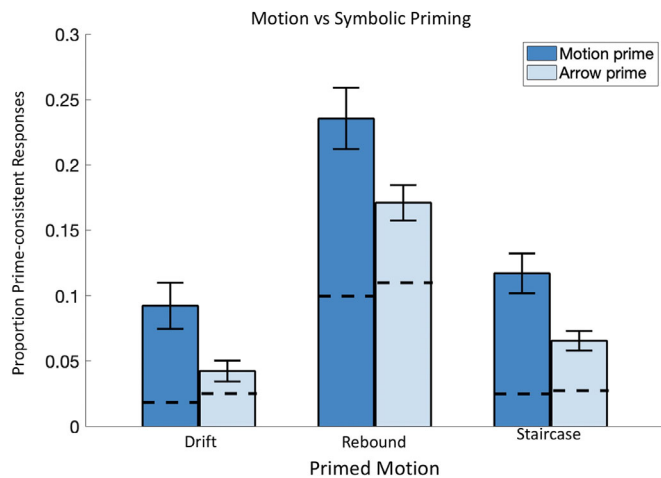


Figure 12. Comparison of prime-consistent responses between motion primes and arrow primes in Experiment 4. Dark blue bars show results following motion primes, and light blue bars show results following arrow primes, shown separately for drift, rebound, and staircase motion types. Dashed lines indicate the overall average proportion of responses of each type across the two blocks of the experiment. Error bars indicate a standard error of the mean across participants.

priming block constitute a successful replication of Experiment 2, indicating that four frames of apparent motion are sufficient to prime drift, rebound, and staircase motion sequences.

We conducted the same analyses for the arrow prime block. Figure 11A shows the distribution of drift responses following drift arrow primes. The diagonal elements (which indicate prime-consistent responses) have a slightly darker blue color than the rest of the cells. To quantify this, Figure 11B compares the average proportion of prime-consistent ( $M = 0.042$ ) and prime-inconsistent ( $M = 0.021$ ) drift responses following drift primes, showing a significantly larger proportion of prime-consistent responses, paired  $t(66) = 4.05$ ;  $p = 0.0001$ , one-tailed; Cohen's  $d = 0.49$ . Similarly, Figure 11C shows the distribution of rebound responses following rebound primes in the arrow prime block. Figure 11D compares the average proportion of prime-consistent ( $M = 0.171$ ) and prime-inconsistent ( $M = 0.100$ ) rebound responses following rebound primes, revealing a significantly larger proportion of prime-consistent responses, paired  $t(66) = 5.85$ ;  $p < 0.0001$ , one-tailed; Cohen's  $d = 0.71$ . Figures 11E and 11F show results for staircase primes. The average proportion of prime-consistent staircase responses ( $M = 0.065$ ), although small, was significantly larger than prime-inconsistent staircase responses ( $M = 0.028$ ), paired  $t(66) = 5.66$ ;  $p < 0.0001$ , one-tailed; Cohen's  $d = 0.69$ . These results show that four frames of symbolic primes (i.e., arrows) are sufficient to prime drift, rebound, and staircase motion sequences.

To directly compare the effectiveness of motion primes and arrow primes at priming drift, rebound, and staircase motion, we conducted a two-way repeated-measures ANOVA with factors of primed direction (three levels: drift, rebound, or staircase) and prime type (two levels: motion or arrow). The results revealed a significant main effect of prime type,  $F(1, 401) = 12.03$ ,  $p = 0.0009$ , and a significant main effect of primed direction,  $F(2, 401) = 54.70$ ,  $p < 0.0001$ , but no significant interaction,  $F(2, 401) = 0.35$ ,  $p > 0.5$ . The main effect of prime type indicated overall more prime-consistent responses during the motion prime block compared with the arrow prime block, and the main effect of primed direction reflects the rebounding bias. Overall, motion primes were significantly more effective at priming motion than arrow primes, and this benefit did not vary as a function of motion type (drift, rebound, or staircase).

## Summary discussion

In the motion prime block, we replicated the results of Experiment 2, showing that four motion priming frames can effectively prime drift, rebound, and staircase motion sequences. In the arrow prime block, we also found evidence of priming for drift, rebound, and staircase sequences, although the effectiveness of the arrow primes was significantly less than the motion primes. Our results do not rule out the possibility that motion primes are tapping into a more abstract, symbolic representation of motion or, vice versa, that symbolic primes such as arrows engage a motion response in their interpretation. Clearly though, including actual motion in the priming stimulus has a greater effect in constraining the subsequent interpretation of maximally ambiguous stimuli.

## General discussion

In four experiments we primed observers with short apparent motion sequences and measured their percepts on two final frames composed of uncorrelated random pixels. In the first experiment, we primed observers with four frames of veridical motion and compared responses across three types of primed motion sequences organized into blocks (drifting, rebounding, and staircase). In each case, we observed evidence of motion sequence priming. However, the block design and the use of specific motion directions left open the possibility that participants used a “global” strategy to develop expectations for the motion sequences that are expected in the context of the study. Such a strategy would contrast with a more direct priming mechanism where the immediately

preceding motion primes the subsequent percepts on a trial-by-trial basis. In [Experiment 2](#), we interspersed trials of drifting, rebounding, and staircase motion sequences and balanced their frequency to avert this possibility. Results showed that staircase motion was indeed primed by the immediately preceding motion, providing novel evidence for two-step motion sequence priming. Further, results of [Experiment 3](#) show that such arbitrary motion sequences are more difficult to prime if the sequence element (e.g., Up–Right) is not repeated at least once. To successfully prime an arbitrary two-step motion sequence such as staircase motion, it is more effective to present at least two consecutive instances of the sequence element (e.g., Up–Right–Up–Right). In contrast, drifting and rebound sequences were primed just as effectively with four or two priming frames. Finally, in [Experiment 4](#) we examined whether real motion is required to produce these priming effects or whether they can be produced just as well by using symbolic primes like static arrows. The results showed that although a sequence of static arrows can indeed prime drift, rebound, and staircase sequences, arrows are considerably less effective than real motion primes at doing so.

### What constitutes a motion sequence?

Contrasting the results of [Experiment 3](#) with those of [Experiment 2](#) strongly suggests that repeating elements determine what constitutes a “sequence” that can be primed. Specifically, showing each motion sequence element at least twice (i.e., at least one repetition of the sequence) leads to stronger priming effects than showing each element only once, for staircase sequences only. This makes sense in the context of predictive processing wherein the priming stimulus has the effect of conditioning one’s expectations ([Rao & Ballard, 1999](#)). For example, in [Experiment 3](#) (with only two priming frames), a veridical percept of Up in the first priming frame was just as likely to be followed by any of the four cardinal directions. If it was followed by Right (thus completing a single element of a staircase pattern), there is little basis on which to expect that a third frame will conform back to Up, or to any other particular direction. Thus, a single presentation of a two-step arbitrary motion sequence does not adequately condition expectations about subsequent motion frames. This ambiguity explains the low proportion of prime-consistent staircase responses in [Experiment 3](#) compared with [Experiment 2](#). However, in [Experiment 2](#), with four priming frames, the expectation of a continuing staircase sequence is established by the repetition of the motion sequence element. When two-step motion elements are perceived to form a *repeating sequence* (e.g., Up–Right followed by another instance of Up–Right), then the motion

sequence is well defined and can be reinstated during subsequent ambiguous frames. Therefore, the property of repetition seems to matter in the degree to which a motion sequence can be primed.

### Top–down sequence expectation

When an expectation has been established based on a spatiotemporal pattern that manifests across multiple frames, it is not difficult to conceive how that spatiotemporal expectation might act to resolve future ambiguous motion stimuli. Previous work has shown that such motion priming can be attributed to attentional selection amplifying certain motion signals (e.g., Up) over competing signals (e.g., Right), effectively conditioning the motion system to be more sensitive to the selected direction ([Raymond, O’Donnell, & Tipper, 1998](#)). These priming effects can be conceptualized as interactions between an intermediate level of processing (attentional selection), and a lower level of processing (directionally selective detectors). Thus, spatiotemporal expectation can be understood as feature-based selective attention reaching down during the test frames to gate midlevel directionally selective circuits that encoded the motion sequence during the priming frames.

However, in order to capture staircase motion priming, this spatiotemporal expectation mechanism would require an additional layer of processing that can guide the feature-based attention to alternately switch between non-opponent directions, such as Up and Right, or more generally between any arbitrary pair of motion directions. In order for the system to predict Up motion on a given frame transition following Up–Right–Up–Right motion, the system would have to “remember” that the motion direction two steps earlier was Up. This additional processing layer would therefore rely on sequence learning mechanisms and is likely to reside in higher order cortical regions where visual working memory can maintain these spatiotemporal motion patterns across multiple frame transitions. Such high-order sequence learning mechanisms have been previously proposed to account for serial order effects in other aspects of learning, as well as in the encoding and physical reproduction of ordered motion sequences ([Lewandowsky & Murdock, 1989](#); [Agam, Bullock, & Sekuler, 2005](#)). Future models of motion priming will thus need to consider the role of visual working memory and sequence learning in addition to feature-based selective attention.

### Open questions

One limitation of our study is that it is difficult to distinguish whether participants are primed to perceive motion or primed to report motion (i.e., a response

bias). This is a general issue with using maximally ambiguous stimuli that are subject to many perceptual interpretations. The inclusion of catch trials with veridical motion was intended to rule out the possibility of a response bias by requiring participants to pay attention to the (potentially real) motion in the last two frames. Further, the occurrence of known response biases across priming conditions (i.e., the rebound bias) suggests that participants were not solely responding in a way to match the priming motion. Still, we cannot rule out the possibility that participants were biased to respond consistently with the primed motion when no other motion information was available in the test frames. Future studies could help disambiguate this by using qualitative measures (such as ratings of confidence, clarity, or vividness) or by examining neural correlates of the perceived motion directions.

The use of maximally ambiguous random pixel arrays presents a methodological opportunity to explore spatiotemporally complex illusory motion sequences. Because sequences of random pixel arrays provide an unconstrained set of motion correspondence solutions, these stimuli afford a much greater range of motion percepts that can be perceived in simpler bistable stimuli or conventional global motion stimuli (Chen, Ashida, Yang, & Chen, 2020). For example, participants in our previous studies have anecdotally reported that these sequences of random pixel frames can lead to percepts of expansion, contraction, rotation, or shear motion (where, for example, the right half moves up while the left half moves down) (Davidenko et al., 2017; see also Hsieh & Tse, 2006). Further, although the current studies only explored priming two-step motion sequences, it seems theoretically possible that longer and more complex motion sequences can also be primed, at least in some observers. The maximum length and complexity of primeable motion sequences and the role that attention and memory plays in motion priming are worth exploring in future research.

## Conclusions

We showed that arbitrary two-step motion sequences (i.e., staircase sequences such as Up–Right–Up–Right) can be primed similarly to drifting motion sequences (e.g., Up–Up) and two-step oppositely coded rebounding sequences (e.g., Up–Down). However, unlike drift and rebound sequences, only staircase sequences were primed more effectively with four priming frames compared with two priming frames, highlighting the importance of repeating the sequence element. Finally, we tested whether symbolic primes (arrows) could also produce priming of motion sequences. We found that, indeed, symbolic primes can constrain the interpretation of subsequent maximally

ambiguous frames. However, we found that motion primes were significantly more effective at producing prime-consistent responses than arrow primes. This result suggests that including real motion information produces a more powerful priming effect.

*Keywords:* apparent motion, priming, motion sequences, higher order motion, multistable stimuli, sequence learning

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## Supplementary material

Supplementary Movie S1. Example of an inconsistent catch trial from [Experiment 1](#). The first four frame transitions depict Up–Right–Up–Right staircase motion, and the final two frame transitions depict veridical Down–Left motion (inconsistent with the priming motion).

Supplementary Movie S2. Example of a real (non-catch) trial from [Experiment 1](#). The first four frame transitions depict Up–Right–Up–Right staircase motion, and the final two frame transitions are completely random.

Supplementary Movie S3. Example of a real (non-catch) trial from [Experiment 3](#). The first frame transitions depict Up–Right staircase motion, and the final two frame transitions are completely random.

Supplementary Movie S4. Example of a real (non-catch) trial from an arrow priming block of [Experiment 4](#). The first four frames show a static pixel array with an arrow flashing a direction four times followed by two final random pixel frames.