Persistent illusory apparent motion in sequences of uncorrelated random dots

Nicolas Davidenko
Department of Psychology, University of California, Santa Cruz, CA, USA

Nathan H. Heller
Department of Psychology, University of California, Santa Cruz, CA, USA

Yeram Cheong
Department of Psychology, University of California, Riverside, CA, USA

Jacob Smith
Department of Psychology, University of California, Santa Cruz, CA, USA

We report a novel phenomenon in which long sequences of random dot arrays refreshing at 2.5 Hz lead to persistent illusory percepts of coherent apparent motion. We term this effect illusory apparent motion (IAM). To quantify this illusion, we devised a persistence task in which observers are primed with a particular motion pattern and must indicate when the motion pattern ends. In Experiment 1 ($N = 119$), we induced translational apparent motion patterns and show that both drifting motion (e.g., up-up-up-up) and rebounding motion (e.g., up-down-up-down) persists throughout many frames of uncorrelated random dots, although rebounding motion tends to persist for longer (a rebounding bias). In Experiment 2 ($N = 60$), we induced rotational IAM on an annulus-shaped display, and show that the topology of the display (whether the annulus is complete or has a gap) determines whether or not the rebounding bias is present. Based on our findings, we argue that IAM provides a powerful tool to study the mechanisms, constraints, and individual differences in the perception of illusory motion.

Introduction

The human visual system is well equipped to detect subtle order in the environment; at the same time, it has an astonishing capacity to impose order where none in fact exists. One of us (ND) experienced a remarkable example of this while participating in a functional magnetic resonance imaging (fMRI) experiment a few years ago. The study involved passively viewing blocks of images presented at 1 Hz, including faces, objects, and finely scrambled images. ND noticed that during the presentation of scrambled images, the scrambled components seemed to move *coherently* across frames, for example shifting up and down, or from side to side. Although these illusory motion percepts would occasionally drift in a single direction (e.g., right-right-right), most often the motion appeared to rebound back and forth (e.g., up-down-up-down). Curious to determine whether other people experienced this phenomenon, ND began to present sequences of randomly refreshing pixel arrays to audiences of students and colleagues, and discovered that under the right spatial and temporal conditions, and with the proper cuing, most people experienced similar illusory motion percepts. Before proceeding, the reader is encouraged to experience this illusory motion phenomenon first-hand by observing Supplementary Video 1 (see also Figure 1; Davidenko, Cheong, & Smith, 2015a, 2015b).

In a recent report (Davidenko et al., 2015b), we showed that such illusory apparent motion (IAM) could be induced in naive participants in a laboratory setting, in the absence of a live presenter. Simply priming observers with several frames containing a drifting (e.g., up-up-up-up) or rebounding (e.g., up-down-up-down) motion pattern at 2.5 Hz was sufficient for that motion pattern to persist across many subsequent random frames. Our data further revealed that for most participants, rebounding motion patterns persisted longer than drifting motion patterns, which we term a "rebound bias."

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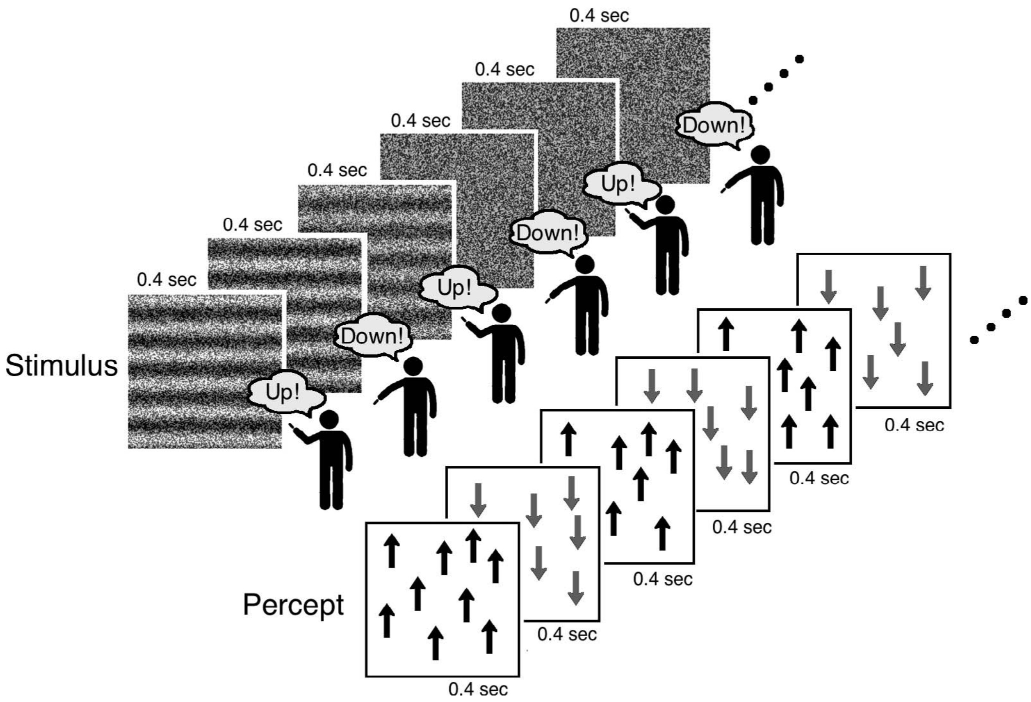

Figure 1. In a live demonstration of the IAM phenomenon, observers are primed to see an up-and-down motion pattern produced by a shifting sine grating superimposed on an array of randomly changing pixels. The presenter reinforces this motion pattern by moving his hand up and down and repeating, “Up! Down! Up! Down!” After several priming frames, the motion signal is removed and observers are left with nothing but randomly refreshing pixels; nevertheless observers continue to perceive up-and-down motion for as long as the presenter keeps repeating those words (and often for much longer). If the presenter suddenly switches to saying, “Right! Left! Right! Left!” observers’ illusory percepts change accordingly. See also Supplementary Video 1.

How can a randomly changing pixel array void of any net motion energy, refreshing at a slow pace of 2.5 Hz, produce persistent illusory percepts of coherent apparent motion (AM)? Further, how can both drifting and rebounding motion patterns be primed in the same paradigm? Finally, why are rebounding motion patterns more robust than drifting motion patterns? To address these questions, we begin by reviewing how priming can serve to disambiguate between competing motion percepts.

Constraining ambiguous AM percepts by priming

AM is the illusion of motion produced by the sequential presentation of two or more static frames. If presented under the right spatial and temporal conditions, the contents of the separate static frames are perceptually unified and interpreted as motion. Consider the simplest possible case: Two frames containing a single dot shifted a short distance apart. When these two frames are presented in alternation at a slow pace (between 1 and 4 Hz; see Finlay & von Grünau, 1987; Selmes, Fulham, Finlay, Chorlton, & Manning, 1997), our motion processing system establishes a correspondence between the content of the two frames, and we perceive motion. For such simple, unambiguous, luminance-defined motion stimuli, arrays of neurons functioning as oriented spatiotemporal filters detect correlations between luminance values across frames, known as *motion energy* (Adelson & Bergen, 1985; Reichardt, 1957; Van Santen & Sperling, 1984). AM can also be computed in the absence of such clear correspondence between features across subsequent frames. Perceiving these types of AM stimuli require that feature extraction take place before motion energy can be computed (Cavanagh & Mather, 1989; Chubb & Sperling, 1988, 1989, 1991; Derrington & Badcock 1985; Lelkens & Koenderik, 1984; Ramachandran, Rao, & Vidyasagar, 1973) or the use of a salience assignment mechanism to distinguish between figure and ground (e.g. Lu & Sperling, 1995a, 1995b, 1996, 2002). By manipulating the informational correspondence between subsequent frames, researchers have identified a number of systematic biases and constraints in our perception of AM (Anstis & MacKay, 1980; Braddick, 1974; Brown, 1931; Gibson, 1968; Kahneman, 1967; Kolers, 1963; MacKay, 1965; Zeeman & Roeflofs, 1953).

We note that a slight modification of the simplest case stimulus can produce an ambiguity that cannot be resolved by motion energy detectors alone. For example, bistable quartets (Anstis & Ramachandran, 1987; Ramachandran & Anstis, 1983, 1985) are similar to the simplest case stimulus described above, with a second dot added to each frame. In each frame, the pair of dots is positioned at opposite corners of a square. When two such frames are presented in alternation at a moderate pace, the motion of the dots falls into one of two mutually exclusive perceptual states: an up-down state or right-left state. Because both interpretations are equally likely, other mechanisms are needed to resolve the ambiguity. As an example of one of these mechanisms, Ramachandran and Anstis (1983, 1985) showed that when priming dots are introduced adjacent to the bistable quartet in a way that is consistent with only one of the two competing states, observers' perception of the quartet is forced into that state. The authors characterized this ambiguity-resolving mechanism as *visual inertia*. The capacity for visual inertia to disambiguate between two competing motion percepts is supported by a number of other priming studies (Jiang, Pantle, & Mark, 1998; Pinkus & Pantel, 1997), which demonstrated a similar effect they termed *visual motion priming* with a three-frame stimulus consisting of luminance-defined sine gratings. The first two frames depicted unambiguous left or right motion by shifting the sine grating by 90° (i.e., one-quarter cycle). The third frame shifted the sine grating by 180° and produced an ambiguous motion signal that could be perceived as either moving left or right. However, observers consistently reported directional motion consistent with the first two frames. Similarly, Jiang et al. (1998) found that when an ambiguously rotating sphere of random dots was primed with an unambiguous depth-defined clockwise or counterclockwise rotation, the ambiguously rotating sphere is seen to inherit the directionality of the priming motion. Although these studies present examples where an ambiguous motion signal is resolved in the same direction as the priming motion, a complex relationship exists between direction of the priming motion and the perceived direction of the subsequent ambiguous stimulus.

Positive and negative effects of motion priming

It has been known for over a century that exposing an observer to a directional motion signal for a long period of time results in a slow illusory motion percept in the *opposite* direction of the adapting motion, known as the motion aftereffect (Wohlgemuth, 1911). For example, when adapting for 30 s to a downward moving waterfall, a static scene appears to slowly drift upward. Motion aftereffect also manifests in changing stimuli. When a flickering ambiguous test stimulus is used instead of a static scene, the effects of motion adaptation can actually be stronger and last longer, depending on the flicker rate and other stimulus parameters (see Bex, Verstraten, & Mareschal, 1996). Indeed, flicker test stimuli have been particularly useful for observing high-level motion mechanisms that cannot be observed on static test stimuli (for example, nearly complete interocular transfer; see Nishida & Ashida, 2000).

The phenomenon we report in this article in some cases exhibits *negative* motion priming (e.g., rebounding motion might be characterized as negative aftereffect occurring on a frame-by-frame basis) but in other cases exhibits the hallmarks of *positive* motion priming (e.g., drifting motion leads to illusory drifting motion in the same direction). Recent work has helped to uncover the complex relationship between positive and negative effects of motion priming (Kanai & Verstraten, 2005; Takeuchi, Tuladhar, & Yoshimoto, 2011; Wexler, Glennerster, Cavanagh, Ito, & Seno, 2013; Yoshimoto, Uchia-Ota, & Takeuchi, 2014). In these studies an unambiguous motion signal is presented for some time, and then one or more ambiguous motion frames are presented—or example, a flickering stimulus whose motion could be interpreted as either left or right. The observer must decide if the motion of the test frames matched or was opposite to the priming motion. These studies revealed that several parameters, including the duration of prime, the velocity of the priming motion, and the duration of the interstimulus interval (ISI) between prime and test, all influence whether the subsequent motion judgment will be positive, negative, or null. For example, Kanai and Verstraten (2005) found that when a priming motion stimulus was presented for durations of 320 or 640 ms, this led to negative priming effects. In contrast, when the priming motion stimulus was presented for shorter durations of 80 or 160 ms, this led to positive priming effects. Importantly, these positive priming effects were only observed with a long enough ISI; with a short ISI, negative priming was observed. Later work by Takeuchi et al. (2011) and Yoshimoto et al. (2014) showed that this relationship depends on an even larger set of stimulus parameters, including the luminance and retinal position of the priming stimulus.

These studies have also served to dissociate between different levels of the motion processing system: between passive, low-level motion processes and active, attention-driven high-level motion processes that occur at a later processing stage. Although both low- and high-level motion systems are vulnerable to priming effects, they respond in different ways and at different time scales. Generally the low-level system is driven by fast motion signals and exhibits negative priming effects. The high-level system is relatively insensitive to fast motion, responding instead to slower or discreet motion signals and showing positive or negative priming effects depending on several stimulus parameters (e.g. Kanai & Verstraten, 2005). We note that in our studies, priming and test stimuli were always presented at 2.5 Hz (each frame lasting 400 ms, with no ISI). At this slow-pace presentation, perception of these stimuli is likely to be vulnerable to attentional effects of the high-level motion system (see General discussion).

Constraining a large space of possibilities to a single motion percept

In these previous studies, the effect of priming is to bias the perception of an ambiguous stimulus that is constructed to have one of two possible interpretations (e.g., leftward or rightward; clockwise or counterclockwise). However, our discovery of IAM suggests that the priming can do more than bias a directionality judgment between two possible solutions; it can produce a globally coherent motion percept out of a field of randomly changing dots, in effect promoting a single coherent motion interpretation out of a large space of possible interpretations. Participants in our studies are not only primed to perceive coherent motion in one or two random frames, but to persist on these illusory percepts for an extended sequence of 10, 15, or more random frames. Most intriguingly, in addition to showing positive priming (e.g., drifting motion), we also show priming of rebounding motion—that is, motion that reverses direction on each frame. Since a rebounding motion pattern can only be defined across at least two frame transitions, it raises the question of whether drifting and rebounding illusory motion percepts arise from the same or different mechanisms.

In this article we present two experiments that elucidate and extend the results of our 2015 findings that are presented in Experiment 1a. In Experiment 1b, we replicate the basic IAM phenomenon in a larger population of participants, and measure whether masking foveal information has any influence on the effect. We show that after observing a few seconds of drifting or rebounding motion, observers continue to perceive the primed motion pattern for many subsequent frames of uncorrelated random dots. We confirm that although both drifting and rebounding motion patterns persist for many frames, rebounding motion reliably persists longer. In Experiment 2, we consider new questions of whether similar illusory percepts can be elicited in rotational motion, and (more importantly) whether the boundary conditions of the display can influence the robustness of rebounding versus drifting motion percepts.

Methods and results

Quantifying IAM: A persistence task

We devised a *persistence* task to measure how long a primed motion pattern persists in the absence of a coherent motion signal. In each trial, participants were presented with an array of random dots refreshing at a frequency of 2.5 Hz (each frame lasting 400 ms, with no ISI). A globally coherent motion signal was present during the first eight or 12 frames, serving to prime a particular motion pattern. After the motion signal was removed, the remaining 24 or 18 frames contained only uncorrelated random dots. Participants were instructed to press a button when they could no longer perceive the primed motion pattern. In each trial, we recorded the delay between the true end of the motion signal and the participant's response. In Experiment 1, we primed drifting or rebounding *translational* AM patterns; in Experiment 2, we primed drifting or rebounding *rotational* AM patterns.

Experiment 1: Priming translational AM

Participants

We recruited 119 participants from the University of California (UC)–Santa Cruz human subjects pool (93 female, 26 male; ages ranging from 18 to 24 years old). The study was approved by the UC Santa Cruz Institutional Review Board. Participants gave informed consent and received course credit for participating. All participants had normal or corrected-to-normal vision. The experiment lasted between 15 and 20 min. Participants were randomly assigned to either Experiment 1a (no foveal mask, $N = 53$) or Experiment 1b (foveal mask, $N = 66$). Portions of the data from Experiment 1a were previously reported in Davidenko et al. (2015b).

Experiment 1a ($N = 53$)

Stimuli

Stimuli were constructed using Matlab and presented using Psychtoolbox3 (Brainard, 1997). In each trial, a *background array* was defined as a 600 × 600 random pixel matrix, with each pixel having a 50% chance of being white or black. The fixed background array

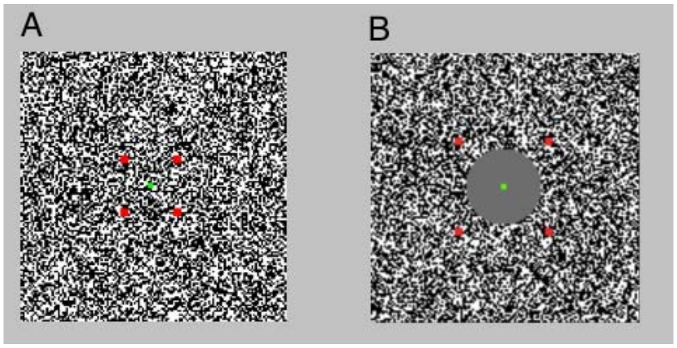

Figure 2. Example stimuli from Experiment 1. (A) Experiment 1a stimuli with green fixation cross and four red dots that reinforce the priming motion during the first six frames of each trial. (B) Experiment 1b stimuli with a masking disc.

served as a sampling space for the *display array*, which was defined as a 140 × 140 pixel window within the background array. Participants only saw the display array fixed in space, surrounded by a solid gray background. By translating the position of the display array across the background array by 4 pixels across frames (much smaller than *d-max* for this stimulus presentation; see Chang & Julesz, 1983), we generated sequences of frames that depicted clear, unambiguous AM. Specifically, we defined the following translational motion primes: *rebounding motion* (either up-down-up-down… or right-left-right-left…) or *drifting motion* (either up-up-up-up… or right-right-right-right…). Stimuli were displayed using Psychtoolbox3 on a 22-in. LCD screen with 60-Hz refresh rate. Participants sat approximately 18 in. from the screen, and the display array subtended approximately 19° × 19° of visual angle.

Procedure

Each trial consisted of a sequence of 32 frames refreshing at 2.5 Hz, with each frame being displayed for 400 ms and immediately replaced by the next frame. The first eight frames contained the motion signal plus 20% noise—that is, each time the display array refreshed, 80% of its pixels shifted by 4 pixels and 20% of its pixel values were rerandomized. The choice of a 4-pixel jump was to ensure that the motion signal was completely unambiguous, and the addition of 20% noise was done to produce a slightly noisy motion pattern that more closely resembled the phenomenological experience of IAM. With 20% noise, the motion signal was still clearly visible and unambiguous. Nevertheless, to reinforce the motion pattern the first six frames contained four red dots that moved in concert with the pixel texture. After the eighth priming frame, the remaining 24 frames in each trial had 100% noise; resulting in a long sequence of uncorrelated random dot arrays (see Figure 2A; Supplementary Video 2).

In each trial, participants observed a particular motion pattern as described above, while fixating on a central green cross. They were instructed to try to see the motion pattern for as long as they could, and to indicate by pressing a key when they could no longer perceive the original motion pattern, at which point the trial ended. Participants were not aware that the transition from 80% coherent motion to pure noise always happened at the onset of the ninth frame. Each participant completed a total of 96 trials (48 trials of drifting motion and 48 trials of rebounding motion).

Results and discussion

We identified four outlier participants based on the distribution of reaction times. These four participants consistently made their responses prior to the end of the motion signal. We obtain the same pattern of results whether or not we include these outliers in the analyses.

For the remaining 49 participants, we report the distribution of responses across the 32 frames of each trial. Figure 3 shows the average distribution of responses across participants, collapsed across the different motion conditions. As the distribution shows, a substantial proportion of responses occur long after the onset of the ninth frame, indicating that the motion patterns persisted for many frames of uncorrelated random dots. Overall, the median response across all participants was 5.7 frames, or about 2.3 s. This median response is much longer than the 300–600 ms it should take participants to prepare and execute a motor response. Remarkably, one out of six trials resulted in persistence of 12 or more frames (5 or more seconds) and in 3.4% of trials, participants did not respond at all, presumably experiencing IAM through all 24 random frames in the trial.

A bias to perceive rebounding motion

Figure 3B shows how the average persistence depends on the primed motion pattern. Although both rebound and drift motion patterns persisted for several frames, we found a significant *rebound bias*, manifesting as longer persistence for rebound motion ($M = 6.2$ frames) compared to drifting motion ($M = 5.1$ frames; paired $t(48) = 4.1$, $p < 0.0001$). Figure 3C shows a scatterplot of individual persistence on rebound trials (y-axis) versus drift trials (x-axis). We note that 39 out of 49 participants (79.6%) exhibited a positive rebound bias, denoted by the points above the $y=x$ line. This rebound bias was not driven by a particular subset of

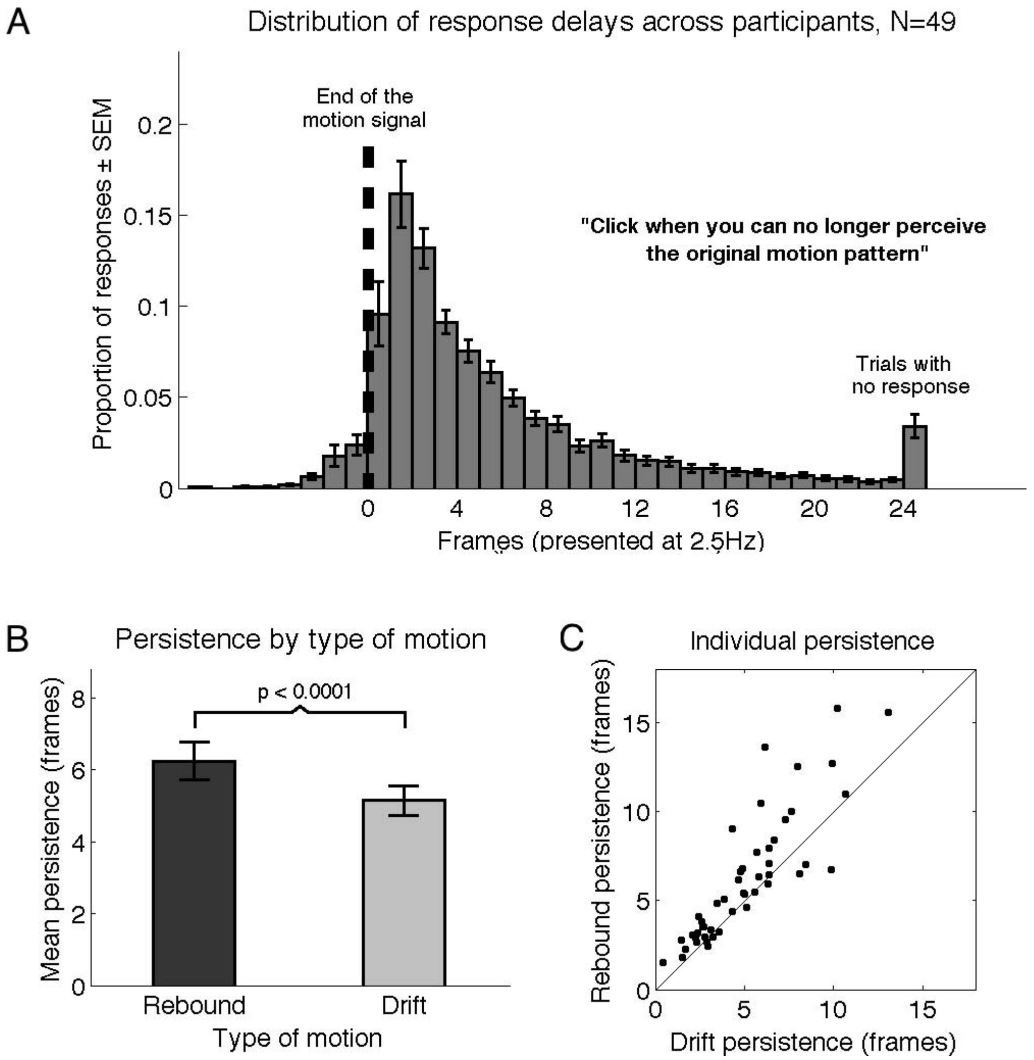

Figure 3. Results of Experiment 1a. (A) Distribution of response delays across 49 observers, collapsed across the different motion conditions. Each bar represents the proportion of responses occurring within a one-frame bin (400 ms). The dark dashed line at $x = 0$ indicates the end of the motion signal (and beginning of the random frames). The bar on the far right indicates the proportion of trials that ended with no response. Error bars denote *SEM* across subjects. (B) Mean persistence across the two types of motion (rebounding and drifting). Error bars indicate *SEM* across subjects. (C) Scatterplot showing the relationship between persistence in drift motion trials (x-axis) and persistence in rebound motion trials (y-axis). The dots that fall above the $y{=}x$ line denote participants who showed a rebound bias (longer persistence for rebound motion trials).

the subject population; rather it was present across the spectrum for both low- and high-persistence observers. This suggests a systematic rebounding bias in the perception of IAM.

We considered the possibility that participants may be using information in the foveal to generate an illusion of coherent motion that spreads across the rest of the random pixel array. Past studies demonstrate that information in the fovea can propagate to the periphery (Ramachandran & Anstis, 1985; Wu, Kanai, & Shimojo, 2004; see General discussion). It is possible that during the random frames in Experiment 1a, participants were resolving a local motion signal in the fovea, which in turn resulted in a globally coherent motion percept across the entire array. In Experiment 1b we used a mask to eliminate any visual motion signal near the fovea and determine whether IAM can still be elicited with only peripheral stimulation.

Experiment 1b ($N = 66$)

Stimuli and procedure

The stimuli and procedure were nearly identical to those in Experiment 1a, except that a solid circular gray mask occluded the central 2.5° around the fixation

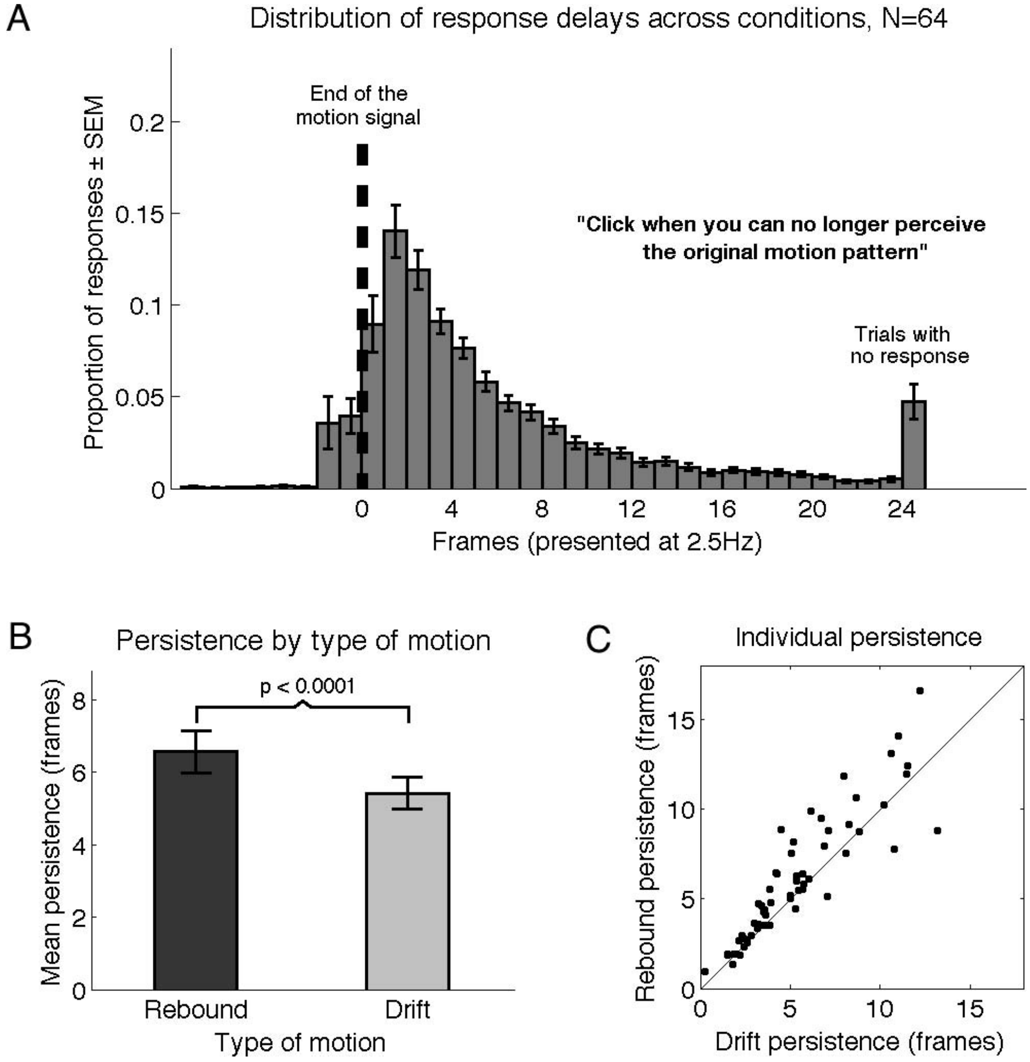

Figure 4. Results of Experiment 1b. (A) Distribution of response delays across 64 observers, collapsed across the different motion conditions. Each bar represents the proportion of responses occurring within a one-frame bin (400 ms). The dark dashed line at $x = 0$ indicates the end of the motion signal (and beginning of the random frames). The bar on the far right indicates the proportion of trials that ended with no response. Error bars denote *SEM* across subjects. (B) Mean persistence across the two types of motion (rebounding and drifting). Error bars indicate *SEM* across subjects. (C) Scatterplot showing the relationship between persistence in drift motion trials (x-axis) and persistence in rebound motion trials (y-axis). The dots that fall above the $y=x$ line denote participants who showed a rebound bias (longer persistence for rebound motion trials).

cross (see Figure 2B and Supplementary Video 3). The red dots that reinforced the motion pattern during the first six frames were spaced slightly farther apart to avoid the gray mask.

Results and discussion

We identified two outlier participants based on the distribution of reaction times. One participant consistently responded prior to the end of the motion signal, and the other never responded before the end of the trial. We obtain the same pattern of results whether or not we include these outliers in the analyses.

For the remaining 64 participants, we report the distribution of responses across the 32 frames of each trial. Figure 4 shows the average distribution of responses across participants, collapsed across the different motion conditions. Again, a substantial proportion of responses occurred long after the onset of the ninth frame. Overall, the median response across all participants was six frames, indicating that IAM persisted on average for about 2.4 s. One out of six trials resulted in persistence of 12 or more frames, and 4.7% of trials led to no response at all. This experiment replicates Experiment 1a, and further shows that persistent IAM cannot be attributed to foveal motion signals spreading to the periphery. Indeed, IAM appears to operate just as strongly when the central region of the display is masked.

As in Experiment 1a, we found a significant rebound bias, manifesting as longer persistence for rebounding motion patterns ($M = 6.6$ frames) compared to drifting motion patterns ($M = 5.4$ frames; paired $t(48) = 4.1$, $p < 0.0001$; see Figure 4B). Figure 4C shows the scatterplot of individual persistence on rebound trials (y-axis) versus drift trials (x-axis). Fifty-one out of 64 participants (79.7%) exhibited a positive rebound bias, remarkably similar to the results of Experiment 1a. Once again, the rebound bias was present both for low- and high-persistence observers: On average rebounding motion patterns persisted for approximately one frame longer than drifting motion patterns. In Experiment 2, we explore a possible source of this systematic rebounding bias by manipulating the topology of the display.

What can account for the rebounding bias that we observed in Experiments 1a and 1b? Work by Hsieh and colleagues (Hsieh, Caplovitz, & Tse, 2005; Hsieh & Tse, 2006) suggested that the boundaries of a display region can influence the directionality of illusory motion percepts. Their work was extension of *illusory line motion* (Hikosaka, Miyauchi, & Shimojo, 1993; Hock & Nichols, 2010; Tse & Cavanagh, 1995) and *transformational AM* (Tse & Logothetis, 2002). In illusory line motion, if a square is replaced by a solid horizontal bar of the same height of the square, the transformation is perceived as motion; the bar seems to shoot out from the square rather than replace the square. Hsieh et al. (2005) discovered that if that bar then changes color, that transformation is also perceived as motion that shoots back in the opposite direction. In fact, presenting bars of alternating colors, at around 2 Hz, leads to percepts of motion that seems to zip back and forth between the left and right edges of the bar, an effect that Hsieh and colleagues termed *illusory rebound motion* (although see Hock & Nichols, 2010, for a discussion of how contrast can influence the directionality of AM). Hsieh, Caplovitz, and Tse (2006) showed similar rebounding motion percepts could also be elicited in square displays densely populated with randomly changing pixels (similar to our stimuli in Experiment 1, but occupying a smaller portion of the visual field and surrounded by a dark boundary). To account for this rebounding motion percept, Hsieh and Tse (2006) posited a *motion continuity heuristic* as an extension of visual inertia: Motion will continue along its current trajectory unless it is obstructed by a boundary, in which case it will reverse direction. Although IAM gives the impression of a shifting surface (rather than motion that zips from one edge of the display to the other), we believe similar spatial constraints may drive the rebound bias in IAM.

Experiment 2: Priming rotational AM

The goal of Experiment 2 was to test the motion continuity heuristic and examine whether the topology of the display array could account for the rebounding bias. When an observer in Experiment 1 was experiencing IAM in the upward direction (for example), that motion might be obstructed by the top edge of the display array, which may increase the likelihood that the illusory motion in the following frame will rebound downward. We hypothesized that a display array whose edges do not obstruct the motion trajectories should eliminate this rebounding bias. To achieve this, we primed rotational motion on an annulus display.

Participants

We recruited 60 participants from the UC Santa Cruz Psychology subjects pool, 45 female, 15 male, ages ranging from 18 to 24 years. The study was approved by the UC Santa Cruz Institutional Review Board. Participants gave informed consent and received course credit for participating. All participants had normal or corrected-to-normal vision. The experiment lasted between 15 and 20 min.

Stimuli

To manipulate the presence of boundaries, in Experiment 2 we created annulus-shaped display arrays (Figure 5) and generated *rotational* motion patterns within these arrays. Several aspects of the stimuli differ from those of Experiments 1 and 2. First, the random dot arrays were blurred using a 2-pixel radius low-pass filter. This blurring served to reduce the salience of vertical and horizontal edges, and facilitate the perception of rotational motion. In addition to the full annulus (Figure 5A) we created two other display conditions: an annulus with a 60° gap on the bottom (Figure 5B), and an annulus with a 120° gap on the bottom (Figure 5C). If the rebounding bias depends on the presence of edges obstructing the path of the illusory motion, the bias should be evident in the two gap conditions, but absent in the full annulus condition. If, on the other hand, the rebounding bias does not depend on the topology of the display array, then it should be observed in all three stimulus display conditions.

A rotational AM pattern was generated using *motion capture*: When a moving luminance-defined grating is superimposed on frames of uncorrelated random dots, the motion of the grating is imputed to the underlying

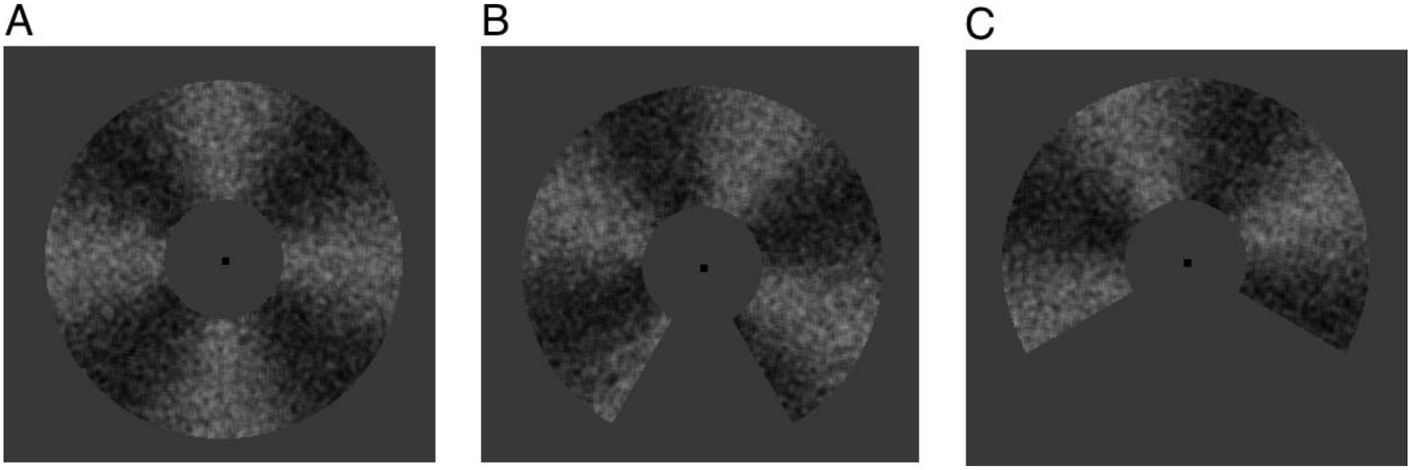

Figure 5. The three display shapes used in Experiment 2. (A) full annulus; (B) 60° gap; and (C) 120° gap. A low-frequency radial sine-wave grating is superimposed on a blurred random pixel array. Over the course of the 12 priming frames, the contrast of the sine-wave grating is gradually reduced to zero, leaving Frames 13 through 30 with only blurred, randomly refreshing pixels.

dots (Ramachandran & Cavanagh, 1987). Here, we superimposed the random dots with a low-frequency radial sine-wave grating that rotated clockwise or counterclockwise by one-quarter cycle (or 22.5° around the annulus) across subsequent frames. This created a clear, unambiguous motion signal depicting either *drifting* rotational motion (clockwise or counterclockwise) or *rebounding* rotational motion (alternating back and forth between clockwise and counterclockwise). Over the course of the first 12 frames, the contrast of the sine gratings was gradually reduced to zero, leaving Frames 13 through 30 with nothing but blurred, uncorrelated random dots (see Supplementary Video 4).

Procedure

The procedure was similar to Experiment 1, but the instructions were slightly different. Participants were asked to fixate on a central cross while observing the rotational AM primes. They were told that the original motion pattern would eventually fade away, and that they should press a key whenever they perceived the original motion pattern to stop or change. As in Experiment 1, we recorded the delay between the end of the motion prime (onset of Frame 13) and the participant's response.

Results

We identified six outlier participants based on the distribution of reaction times. Two participants consistently responded prior to the end of the motion signal, and four participants never responded before the end of the trial. We obtain the same general pattern of results whether or not we include these outliers in the analyses.

For the remaining 54 participants, we report the distribution of responses across the 30 frames of each trial. Figure 6A shows the average distribution of response delays, collapsed across participants and conditions. Note that the distribution looks different from that in Experiment 1 in that it does not spike sharply when the motion signal ends. This is because the sine grating that carries the motion signal has been fading gradually, rather than suddenly. We estimate that it becomes undetectable for most observers between the ninth and 11th frame. This variability across observers manifests as a gradual rise in the average response distribution during the 2 or 3 final frames of the motion prime (indicated by the light gray bar in Figure 6A). Nevertheless, the results clearly show that rotational AM can be primed using motion capture, and that it persists throughout many subsequent frames of uncorrelated random dots. In fact, the overall median persistence was 7.5 frames (or 3 s), somewhat longer than in Experiment 1. One in four trials led to persistence of 13 or more frames (5 or more seconds), and a remarkable 18.4% of trials ended with no response. These results indicate that illusory rotational motion can persist as long as or longer than illusory translational motion.

To test the hypothesis that the rebound bias observed in Experiment 1 is due to the presence of boundaries obstructing the perceived motion trajectories, we compared the mean delay across the three stimulus boundary conditions: full annulus, annulus with 60° gap, and annulus with 120° gap. Consistent with this hypothesis, we found a significant rebounding bias in both the 60°-gap, $t(53) = 3.20$, $p = 0.002$, and 120°-gap, $t(53) = 2.56$, $p = 0.01$, conditions, but no

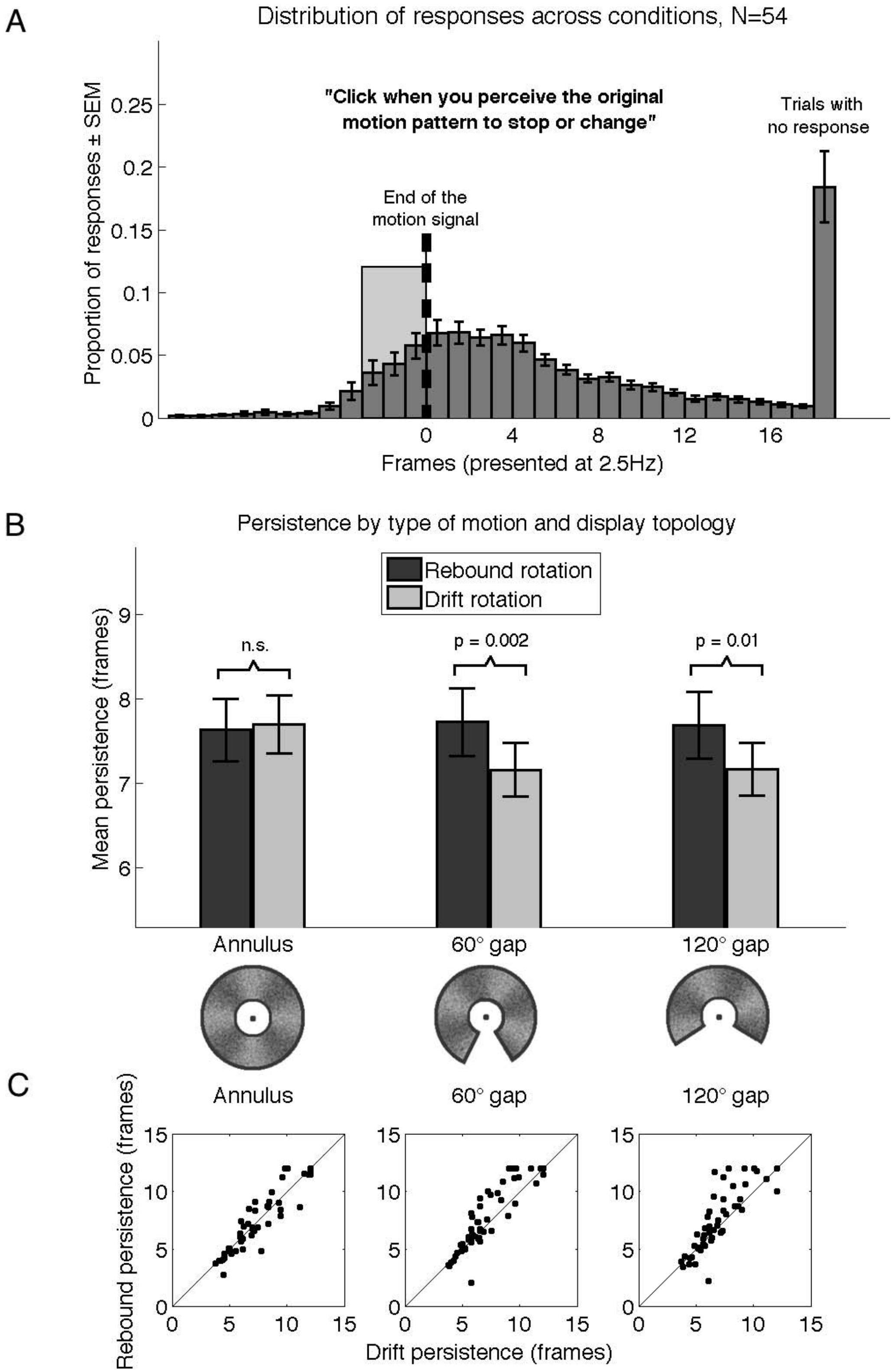

Figure 6. Results of Experiment 2. (A) Distribution of response delays across 54 observers, collapsed across the different motion conditions. Each bar represents the proportion of responses occurring within a one-frame bin (400 ms). The dark dashed line at $x = 0$ indicates the end of the motion signal (and beginning of the random frames). Note that the sine grating becomes difficult to detect starting three frames earlier, indicated by the light gray bar. The bar on the far right indicates the proportion of trials that ended with no response (18.4% of trials). Error bars denote *SEM* across subjects. (B) Mean persistence across the two types of motion (rebounding and drifting) and the three types of display shapes (annulus, 60 gap, 120 gap). Error bars indicate *SEM* across subjects.

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The p values indicate significance of t test comparing whether rebound motion persists statistically longer than drift motion. (C) Scatterplots showing the relationship between persistence in drift motion trials (x-axis) and persistence in rebound motion trials (y-axis). The dots that fall above the $y=x$ line denote participants who showed a rebound bias (longer persistence for rebound motion trials).

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rebounding bias in the full annulus condition, $t(53) = -0.49$, $p > 0.5$ (see Figure 6B). Figure 6C shows a scatterplot of individual persistence on rebound trials (y-axis) versus drift trials (x-axis) across the three stimulus conditions. In the full annulus condition, only 23 of 54 participants (42.6%) exhibited a rebound bias. In contrast, 34 participants (63.0%) exhibited a rebound bias in the 60°-gap condition, and 33 participants (61.1%) exhibited a rebound bias in the 120°-gap condition. Overall these results support the view that the rebounding bias is due at least in part to the presence of a boundary obstructing the illusory motion trajectory.

General discussion

Summary of results

Our experiments show that following a priming motion pattern, sequences of uncorrelated random dots refreshing at a slow pace of 2.5 Hz can elicit persistent IAM that maintains the primed motion pattern. Across two experiments with 167 participants, we demonstrated that both translational and rotational IAM can be induced in a similar way, and that both drifting and rebounding motion patterns can persist throughout many subsequent random frames. In Experiment 1, using translational motion on a square pixel array, our data also revealed a rebounding bias, in which for most observers rebounding motion patterns persisted longer than drifting motion patterns. In Experiment 2, using rotational motion on an annulus display, we provided evidence that this rebounding bias depends on the topology of the display; the rebounding bias is evident whenever the display array includes boundaries that obstruct the trajectory of IAM, but disappears in the absence of such boundaries. Finally, our data demonstrate the robustness of IAM. Across the two experiments we varied the nature of the priming motion direction (translational vs. rotational motion), the source of the motion signal (rigid translation with noise vs. motion capture), the way the priming phase ended (suddenly vs. gradually), and the task instructions ("try to perceive the motion pattern as long as possible" vs. "indicate when the original motion stops or changes") and found evidence of persistent IAM across these manipulations.

The use of rotational motion in Experiment 2 further allowed us to discount possible effects of eye movements. Although participants were instructed to fixate on a central cross in all of our studies, we do not have eye-tracking data to confirm whether all participants followed these instructions. In the case of translational motion in Experiment 1, it is possible that some participants made eye movements between frames that facilitated the perception of AM. However, such a mechanism cannot account for rotational motion percepts experienced in Experiment 1. Directional saccades would only lead to the perception of translational motion, not rotational motion. We therefore conclude that eye movements are not necessary to experience IAM.

Despite the robustness of IAM, there was considerable variability across participants. By examining these effects in 167 naive participants, we were able to find a wide range of individual differences in the persistence of IAM. Figure 7 shows the distributions of median persistence for participants in Experiment 1 (collapsing data from Experiments 1a and 1b; Figure 7A) and for participants in Experiment 2 (Figure 7B). The distributions show that participants vary widely in how many frames IAM typically lasts, with some participants experiencing only two or three frames of illusory motion, and others experiencing persistence of 10, 15, or even more frames. As we consider later, this variability across participants may reflect individual differences in the ability to attentionally track complex and changing stimulus features at 2.5 Hz. Alternatively the variability may reflect different criteria that individuals apply when deciding what counts as coherent motion (see Whitson & Galinsky, 2008).

The persistence task we devised for these experiments asked participants to report when a priming motion stopped or changed. Participants' mean response delays of six to seven frames (or 2.4–2.8 s) therefore indicate that they continued to perceive the same primed motion pattern for many subsequent random frames. What mechanisms may be responsible for perceiving a primed globally coherent motion pattern in frames of uncorrelated random dots?

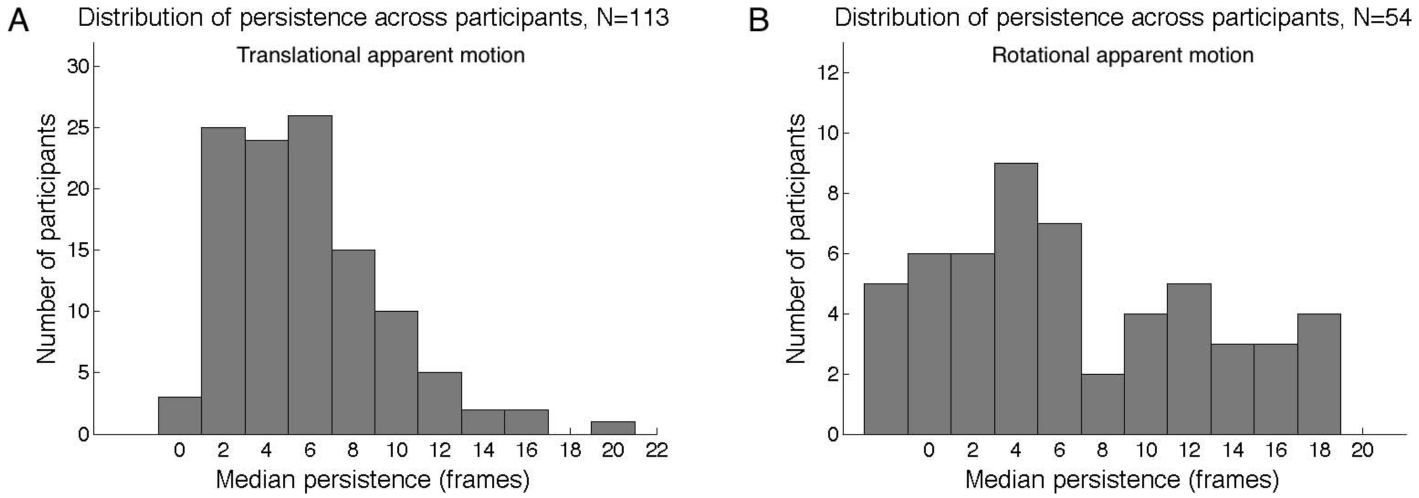

Figure 7. The distribution of individual persistence, measured as the median number of random frames elapsed before a participant responds. (A) Results from 113 participants from Experiments 1a and 1b combined, measuring IAM in translation motion. (B) Results from 54 participants from Experiment 2 measuring IAM in rotational motion. Negative values indicate observers' whose median responses occurred before the motion signal had completely faded.

Perceiving globally coherent motion from random noise

One mechanism that may lead to the illusion of globally coherent motion from random noise is that observers resolve global motion ambiguities using local motion information. Ramachandran and Anstis (1985) demonstrated such local-to-global propagation using fields of bistable AM quartets. They showed that whenever a fixated quartet was perceived to change states (e.g. from a north-south state to an east-west state), all the peripheral quartets appeared to change along with it, creating a globally coherent motion pattern. In a later study, Wu et al. (2004) discovered a similar local-to-global propagation phenomenon using fields of continuously moving red and green dots. They found that when participants fixated in the center (where red dots moved up and green dots moved down), the dots in the periphery seemed to inherit this motion (although in reality the peripheral dots moved in the opposite way). In these studies, foveal information was shown to spread peripherally. Since Experiments 1b and 2 included a mask to obscure foveal information, the source of local motion would have to itself originate somewhere other than the fovea. Watanabe and Cole (1995) provided evidence of peripheral propagation by examining an array of apparently moving dots that were perceived as drifting in the center of the array but oscillating in the edges of the array. They showed that when participants attended to the oscillating dots at the edges, the center dots inherited the oscillating motion pattern. Therefore, it seems plausible that a global propagation mechanism may help to produce a coherent motion pattern in the entire array from local motion information.

The role of attention

Although global propagation may account for how an entire display can inherit a local motion pattern, it leaves open the question of how, in a purely random stimulus, a local motion pattern is established in the first place. Previous research has shown that when two competing motion signals are superimposed, an attention-based motion process can serve to disambiguate and promote one dominant directional signal (Anstis & Ramachandran, 1987; Cavanagh, 1992; Culham & Cavanagh, 1994; Culham, Verstraten, Ashida, & Cavanagh, 2000; Durgin, 2002; Lu & Sperling, 1995b; MacKay, 1965; Ramachandran & Anstis, 1983; Wertheimer, 1912; Verstraten, Cavanagh, & Labianca, 2000). For example, Cavanagh (1992) devised a paradigm that pitted a luminance-defined motion signal against a color-defined motion signal, rotating in opposite directions on an annulus display. During passive viewing, the luminance-defined grating generally drove the global motion percept, but when participants attentionally tracked the color bars, the attended motion signal dominated. The color bars provided a consistent feature that the attention-based system could track across frames. In later work, Culham and Cavanagh (1994) showed that when participants attended to either a color- or luminance-defined grating superimposed on a field of randomly changing dots, the motion of the attended gratings "captured" the motion of the underlying random dots. Particularly relevant to our findings, this capture mechanism held even when the tracked motion signal was itself ambiguous and need to be resolved by attention. Verstraten et al. (2000) showed that this type of attentional tracking breaks down at flicker rates higher than around 4–8 Hz (where the specific limit varied considerably across the individuals tested). We note that, although our presentation rate of 2.5 Hz falls below this threshold, it is possible that different individuals within our subject population have different attentional tracking thresholds. For some participants the presentation rate of 2.5 Hz may have been too fast for their attentional tracking system to generate IAM. This variable sensitivity to frequency may be one source of the large individual differences in persistence we found across observers.

Because our stimuli were not simply composed of two discernable motion signals tied to consistent stimulus features like color or luminance, the attention-based motion system must solve an additional problem in order to generate IAM from random noise. The uncorrelated frames provide a large space of competing motion signals, and an undeterminable set of features (pixels or clusters of pixels) that could potentially correspond between one frame and the next. In a given frame transition, observers may establish an (imperfect) correspondence between a cluster of pixels across in N and a similar cluster of pixels in Frame $N+1$. Indeed, previous work has shown remarkable flexibility in how correspondences can be established between differing stimulus features (e.g., Schiller & Carvey, 2006). However, observers may need to attend to a different cluster of pixels to establish a correspondence between Frames $N+1$ and $N+2$. Therefore, in order to sustain *persistent* illusory motion that survives across many random frame transitions, the system must be dynamically flexible in which features are tracked and corresponded from frame to frame.

Are drifting and rebounding motion supported by the same or different mechanisms?

If an attention-driven dynamic feature selection system, combined with a local-to-global propagation mechanism, can produce coherent motion percepts from random noise, how can we account for the fact that both drifting *and* rebounding motion are produced in the same paradigm? We posit that drifting motion (both translational and rotational) may be an extension of the positive priming effects we discussed earlier. By presenting several frames depicting motion in the same direction at 2.5 Hz, the high-level system is primed to keep perceiving that direction of motion when presented with ambiguous information. Even though the subsequent frames are entirely random, the priming effects at 2.5 Hz seem to be strong enough to produce a persistent illusion of motion that continues along the primed direction. Although it is possible that rebounding motion arises through a similar mechanism, we consider three different possibilities below.

Rebounding motion results from priming a two-step motion pattern

One way rebounding motion can be elicited is if the attention-based system can be primed over a larger set of motion steps. As our studies demonstrate, the direction of the illusory motion on the first random frame cannot be determined by the motion on the last priming frame alone; it is also influenced by the direction of motion on the second-to-last priming frame. For example, if the last two priming frames are down-up, the first illusory frame will be perceived as down (rebounding motion). In contrast, if the last two priming frames are up-up, the first illusory frame will be perceived as up (drifting motion). Therefore, if rebounding motion is supported by the same type of priming mechanism as drifting motion, the priming would need to operate over a two-step motion pattern. This possibility raises the interesting question of whether *nonrebounding* two-step motion patterns (e.g. up-right-up-right) can also be primed. If a two-step, nonrebounding motion pattern such as this can be primed and sustained as robustly as a rebounding motion pattern, that would suggest that the attention-driven system can indeed operate over a complex, two-step motion pattern. Perhaps under the right spatio-temporal conditions, even more complex motion patterns (such as three- or four-step motion) can also be primed. Future work may examine the scope of motion complexity that can be primed and subsequently sustained as IAM.

Rebounding motion results from spatial constraints and boundaries

Alternatively, rebounding motion may be the result of spatial constraints of the attention-based system and sensitivity to boundaries. In early work, Wertheimer (1912) presented a simple ambiguous AM stimulus by alternating a cross with an X. He noticed that although with attentional tracking the stimulus could be perceived to rotate clockwise or counterclockwise, under passive viewing the motion seemed to rock back and forth. As noted by Verstraten et al. (2000), such back and forth motion might represent "the least effortful path along which attention may be drawn" (p. 3663). This implies that back-and-forth motion is a particularly stable attentional state. Supporting this idea, research by Hock, Kelso, and Schoner (1993) showed that alternating motion patterns are resistant to change. When observers were presented with an asymmetrical bistable quartet, motion was perceived between pairs of dots that were closer in space, known as the "proximity rule." Hock et al. (1993) showed that if the distance between the dots was gradually increased past the point of equality, the original percept was nevertheless maintained, indicating the stability of the original back-and-forth percept.

As we discussed earlier, work by Hsieh and colleagues (Hsieh et al., 2005; Hsieh & Tse, 2006) showed that spatial boundaries can facilitate illusory rebounding motion in stimuli with no net motion energy. Our results from Experiment 2 (where the rebound bias exists in the two gap conditions with boundaries but not in the full annulus condition), support the idea that boundaries can account for the more robust persistence of rebounding motion compared to drifting motion. Nevertheless, our observers still experienced persistent rebounding motion in the full annulus condition (where there were no boundaries that interfered with the rotational motion). This suggests that boundaries, while playing a facilitative role, are not necessary for the perception and maintenance of rebounding motion.

Rebounding motion results from frame-to-frame motion adaptation

Finally, it is possible that illusory rebounding motion is the result of an adaptation-like process that occurs from one frame to the next. For example, perceiving (illusory) upward motion in one frame might adapt up-sensitive detectors, and cause the subsequent frame to be perceived as moving down; this in turn would adapt down-sensitive detectors and cause the following frame to be perceived as moving up, and so on. If this were the case, these negative priming effects would need to be finely tuned, such that they are strong enough to maintain rebounding motion percepts when they are primed, but not so strong as to suppress drifting motion percepts when those are primed—that is, to successfully prime drifting motion, the priming would need to be strong enough override the tendency for motion to rebound due to adaptation. This suggests that the relative parity we observed between drifting and rebounding persistence may be fragile and would be disrupted with different stimulus manipulations.

If drifting and rebounding motion are driven by different mechanisms, it should be possible to dissociate them by manipulating certain stimulus properties. For example, increasing the frame rate might increase the effects of frame-to-frame adaptation and therefore diminish the persistence of drifting motion. Alternatively, based on the work by Kanai and Verstraten (2005) that showed positive priming effects build over time, increasing the number of priming frames would likely increase the persistence of drifting motion, but may not influence the persistence of rebounding motion (as long as there are at least three priming frames to initiate the process). Finally, the coherence of the motion signal in the priming frames might have differential effects on the two types of illusory percepts. If maintaining drifting IAM requires more attentional effort, then perhaps a noisier motion prime (that requires more attention to track) might be more effective in producing drifting IAM than a stronger motion prime (that can be perceived more passively). Future studies may pursue these questions to resolve which factors influence the persistence of drifting versus rebounding motion and determine to what extent these percepts depend on different levels of motion processing.

Conclusion

Although we have considered potential mechanisms to explain some characteristics of IAM, there are still many unexplored aspects of the phenomenon that warrant further investigation. For example, in addition to the translational and rotational motion percepts we have described here, some observers also report percepts of expanding/contracting motion or shearing motion (where, for instance, the left and right halves of the display appear to move in opposite directions). Hsieh et al. (2006) also noted that some of their participants reported a variety of motion percepts when presented with arrays of randomly refreshing dots. In addition to exploring the types of motion patterns that can be illusorily perceived, future research may also investigate whether other types of attentional cuing can also elicit IAM in the absence of a visual motion prime. Although we always primed our participants using real motion, as we alluded to in the introduction, the cuing of the attention-based motion system can also be accomplished using words (e.g., "Up! Down! Up! Down!"). By using stimuli with no net motion energy that can nevertheless elicit persistent illusory percepts of coherent motion, we believe that IAM provides a simple but powerful tool to investigate how motion is created from noise.

Keywords: apparent motion, *higher order motion*, *priming*, *persistence*, *illusory apparent motion*

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Corresponding author: Nicolas Davidenko.
Email: ndaviden@ucsc.edu.
Address: Department of Psychology, University of California, Santa Cruz, CA, USA.

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