# Believable change: Bistable reversals are governed by physical plausibility

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Planar motion flows can induce the illusory appearance of a volume rotating in depth ("depth from motion"; G. Sperling, & B. A. Dosher 1994). This appearance changes spontaneously from time to time, reversing simultaneously its depth and its direction of rotation. We investigated *asymmetric* illusory volumes, which reverse more frequently at some angles of view than at others. In three experiments, we studied spontaneous joint reversals of depth and motion, as well as induced reversals of either motion or depth alone. We find that depth reversals occur exclusively when the illusory volume is depth symmetric (so that the shape of the volume remains unchanged). In contrast, motion reversals occur at all view angles, but their frequency varies with the motion speed. The probability of joint reversals is well approximated by the product of the individual reversal probabilities, suggestive of two independent random processes. We hypothesize that reversals of illusory volumes are conditioned by prior experience of physical transformations in the visual world.

## Introduction

When observers view an ambiguous visual scene, perception alternates spontaneously between rivaling interpretations. This phenomenon of "multistable perception" has been studied scientifically since the 19th century (von Helmholtz, 1866; Wheatstone, 1838) and has been described for many types of visual displays, including Necker cubes and similar ambiguous figures (Necker, 1832), depth-from-motion displays (Sperling & Dosher, 1994; Wallach & O'Connell, 1953), monocular and binocular rivalry (Blake & Logothetis, 2002; Leopold & Logothetis, 1999; Tong, Meng, & Blake, 2006), and others. Perceptual reversals are thought to be triggered when the balance between competing neural representations shifts, for example, due to neural adaptation, spontaneous activity fluctuations, attention shifts, or other factors (Kang & Blake, 2010; Kim, Grabowecky, & Suzuki, 2006; Lankheet, 2006; Mitchell, Stoner, & Reynolds, 2004).

In general, the stability of a "dominant" perceptual state is thought to reflect the balance between its neural representation and the representations of the alternative ("suppressed") states. For example, a selective increase of the neural activity associated with the dominant percept (by increasing either stimulation or attention) is known to stabilize this percept (Chong, Tadin, & Blake, 2005; Lankheet, 2006; Levelt, 1965). Measures that retard neural adaptation of the dominant percept (by reducing stimulation/attention, by moving the stimulus to unadapted locations, or by interrupting stimulation) also serve to stabilize this percept (Adams, 1954; Blake, Sobel, & Gilroy, 2003; Levelt, 1965; Orbach, Ehrlich, & Heath, 1963; Pastukhov & Braun, 2007, 2008). In short, multistable phenomena are typically analyzed in terms of competing perceptual states (or their associated neural representations).

However, not all aspects of multistability can be understood in these terms. When the illusory volume in a depth-from-motion display is not rotationally symmetric, stability of the illusory percept varies with rotation/phase angle (Brouwer & van Ee, 2006; Jackson, Cummins, & Brady, 2008; Wallach & O'Connell, 1953). This sits oddly with the notion that stability reflects simply a balance between alternative perceptual states. Depth-from-motion displays are perfectly ambiguous at all phase angles (Figure 1). Thus, the two alternative interpretations are always evenly balanced and it is not apparent why the stability of the dominant percept should change with the rotational state.
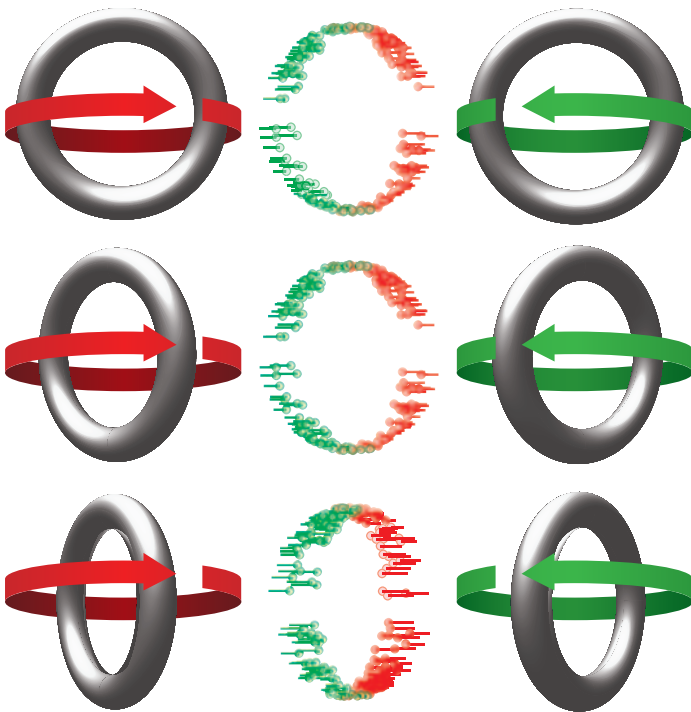
Figure 1. Ambiguity in depth from motion. A planar flow (center) is perceived as one of two illusory volumes rotating in depth (left or right). Note that the two alternative volumes differ in two aspects: illusory depth (shading) and illusory motion (arrows). At any given rotational angle, the alternative illusory volumes are equally plausible (see also Movies 1–5).

Here, we investigate the reasons for the puzzling angular dependence of illusory depth from motion (Brouwer & van Ee, 2006; Jackson et al., 2008; Wallach & O'Connell, 1953). The logic of our study is illustrated in Figure 2. In the case of spontaneous reversals, two phenomenal attributes of the illusory volume—depth and motion—always reversed simultaneously. In general, the frequency of such reversals depended on the phase angle of the illusory volume (Figure 2A).

To dissociate reversals of depth and motion, we instantaneously inverted the planar motion flow, so that the illusory volume was no longer consistent with the planar flow (Figure 2B). In response, the illusory volume sometimes reversed depth and maintained (the original) motion. This manipulation served to isolate reversals of illusory depth (and their dependence on phase angle). Similarly, by transiently adding conflicting stereoscopic depth to the planar flow, the illusory depth could be inverted temporarily (Figure 2C). In response, the illusory volume sometimes reversed motion and maintained (the inverted) depth. This second manipulation served to isolate reversals of illusory motion (and their dependence on phase angle).

Our results showed that the transformations of illusory depth and of illusory motion were governed by different rules: The former depended on depth symmetry in an all-or-nothing fashion, whereas the latter depended on motion speed in a graded fashion. We hypothesize that these differences reflected the disparate physical plausibility of such volume transformations in the natural visual world.

## Methods

### Observers

Seven observers (including the first and second authors, three females, four males) participated in all three main experiments. Procedures were approved by the medical ethics board of the Otto-von-Guericke-Universität, Magdeburg and informed consent was obtained from all observers. All observers had normal or corrected-to-normal vision. Apart from the authors, observers were paid to participate and were naive as to the purpose of the study.

### Apparatus

Stimuli were presented on a 21″ CRT screen with a spatial resolution of $1600 \times 1200$ pixels and a refresh rate of 100 Hz. For natural viewing, the viewing distance was 70 cm, with 1 pixel subtending approximately 0.19°, and the background luminance was 35 cd/m$^2$. For dichoptic viewing (mirror stereoscope), the viewing distance was 87.5 cm (1 pixel subtending 0.014°) and the background luminance was 35 cd/m$^2$.

### Stimuli

Planar motion flows induced the illusory appearance of three-dimensional volumes rotating in depth ("depth from motion"; Sperling & Dosher, 1994; Wallach & O'Connell, 1953). To create these flows, 2000 bright dots (diameter of 0.1°, luminance of 80 cd/m$^2$, infinite lifetime) were distributed over (all or part of) the front and back surfaces of a virtual sphere rotating about its vertical axis and were projected orthographically onto the image plane. To create single, double, or quadruple rings, dots were placed on one, two, or four circumpolar bands spaced evenly along the equator, each with a width of 1/16 of a circumference (Figure 3, Movies 1–5 and 8). Depending on the fraction of the spherical surface covered by dots, local dot density differed between shapes. In addition, to favor a unitary
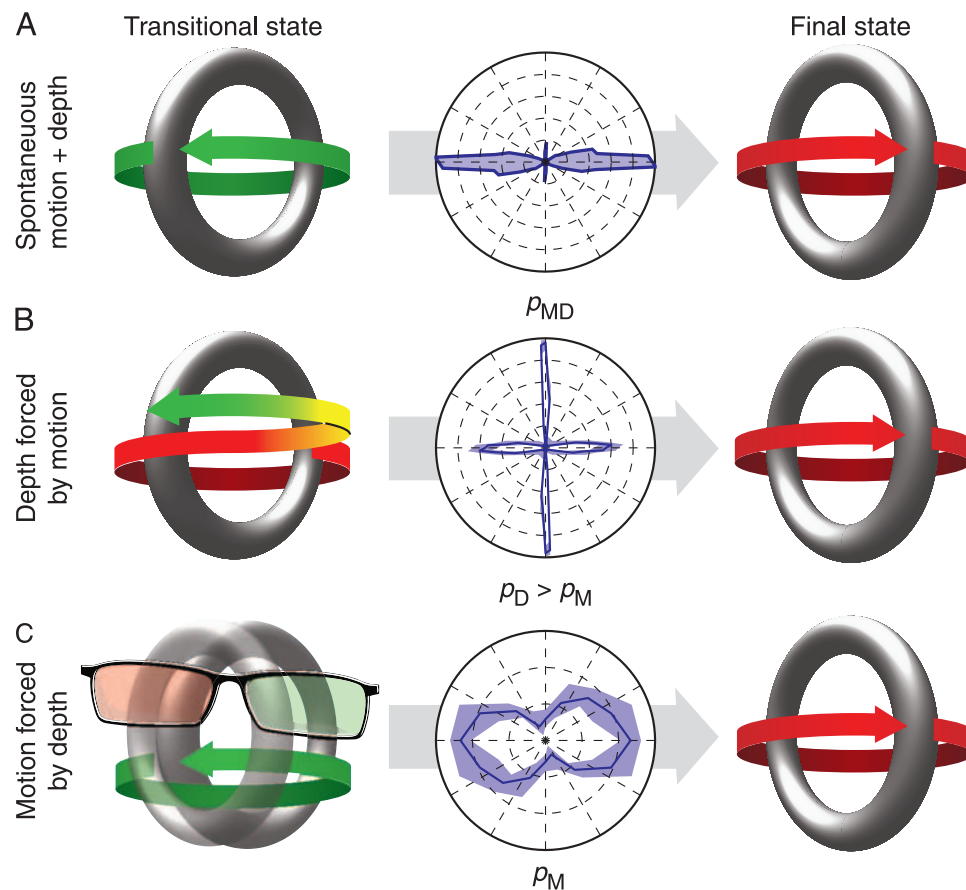
Figure 2. Paradigm and selected results. Results are presented as polar plots (i.e., as viewed from the axis of rotation). (A) Spontaneous reversal of illusory depth and motion, polar plot of relative probability $p_{MD}$ as a function of rotation angle $\alpha$. Reversals occur mostly at two angles: fully frontal and (very rarely) edge on. (B) Spontaneous reversal of illusory depth, following forced transition of planar motion (inverted 2D motion), relative probability $p_D$ as a function of rotation angle $\alpha$. Illusory depth reversals occur only at two angles: fully frontal and edge on. (C) Spontaneous reversal of illusory motion, following forced transition of depth (inverted binocular disparity), relative probability $p_M$ as a function of rotation angle $\alpha$. Illusory motion reversals occur at all angles, but the probability varies smoothly between a maximum (fully frontal) and a minimum (edge on).

illusion, local dot density was higher near the poles. The virtual sphere was centered on fixation and measured 4.7° in radius. The frequency of its rotation about the vertical axis was 0.25 Hz.

## Procedure

### Continuous presentation

In order to confirm that all selected stimuli were bistable, observers viewed stimuli continuously for 2 min while reporting on perceived direction of rotation (pressing *left* for leftward rotation, *right* for rightward, and *down* for mixed percept; <1% of all reports). Mean duration of dominance phases and correlation with cumulative history

(see Pastukhov & Braun, 2011 for details) are presented in Figure 4.

## Experiment 1

In this experiment only, a large yellow dot (eccentricity of 10° and diameter of 2°) accompanied the main stimulus, serving as a clock. It circumnavigated the main stimulus with a frequency of 0.25 Hz, starting at a randomized position in each trial. Observers viewed the display continuously and awaited a spontaneous reversal in illusory appearance (depth and motion). Upon noticing such a reversal, they memorized the position of the clock dot and pressed the *Space* key, thereby removing the main display and stopping the clock dot. Thereafter, they used *arrow* keys to return the clock to the position it had occupied at the moment of the reversal. Five stimuli—uniform sphere,
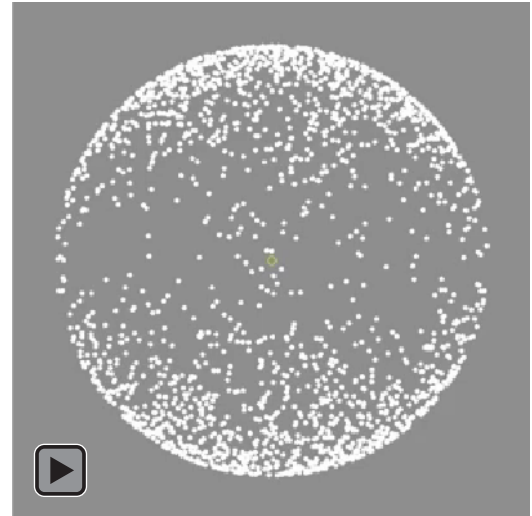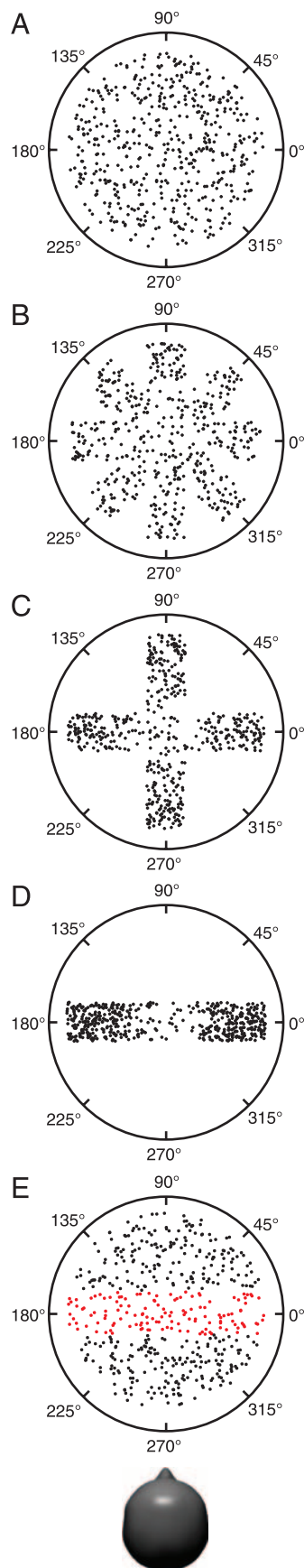
Movie 1. Uniform sphere.

four-band, double-band, single-band, and color-band—were used in this experiment and observers performed 120 trials with each stimulus. Trial duration depended on the average dominance phase duration for a given observer and stimulus (range of 3 to 15 s plus response interval).

The distributions of response times and of estimated switch times for the single-band stimulus are shown in Figure 5. All times are relative to the instant at which the phase angle was 0° or 180°. Note that the distribution of estimated switch times is more symmetric than that of response times (skewness $\gamma = 0.05$ compared to $\gamma = 1.1$ for RT), has a smaller variance ($\sigma = 156.4$ ms compared to $\sigma = 250$ ms for RT), and has an almost zero mean ($\mu = 31$ ms compared to $\mu = 636$ ms for RT).

## Experiment 2

Observers viewed a planar motion flow for 1500 ms. At a random time between 500 ms and 1000 ms, all dots inverted their motion. This inversion occurred at selected phase angles, which were grouped around the major symmetry axes (on the basis of pilot experiments). Specifically, the investigated phase angles were 0°, 2.5°,



Figure 3. Displays (schematic). Dots covered all or part of a spherical surface, here viewed from the axis of rotation. All displays are depicted at an angle of rotation of 0°, relative to an observer positioned at 270° (pictured at bottom). The actual displays are available as Movies 1–5 (please set looped presentation). (A) Uniform sphere (Experiment 1). (B) Four intersecting bands (Experiment 1). (C) Two intersecting bands (Experiments 1–3). (D) Single band (Experiments 1–3). (E) Full sphere with a color band (Experiment 1).
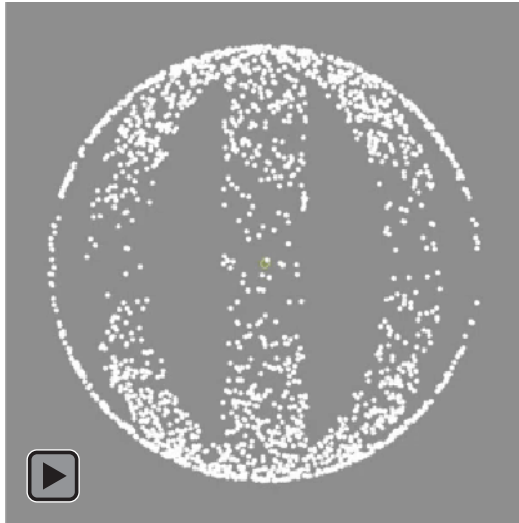
Movie 2. Four-band stimulus.
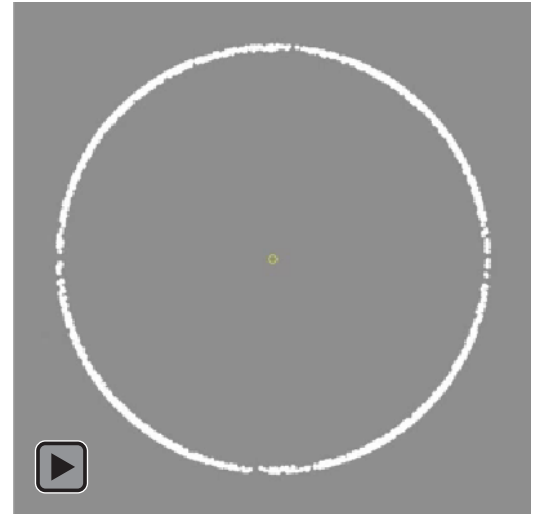


Movie 4. Single-band stimulus.

4°, 5°, 10°, 22.5°, 35°, 40°, 41°, 42.5°, 45°, 47.5°, 49°, 50°, 55°, 67.5°, 80°, 85°, 86°, 87.5°, and 90° for the two-band display and 0°, 2.5°, 5°, 10°, 45°, 80°, 85°, 87.5°, and 90° for the one-band display. Observers reported whether the illusory volume did or did not invert its rotation. A change in the illusory rotation implied that *no change* was perceived in the illusory depth (Movie 6). Symmetrically, no change in illusory rotation implied that the physical discontinuity of motion was compensated by a change in illusory depth (Movie 7, red dots were not present in the original display and were added only to make detection of depth reversal easier). Only double-band

and single-band stimuli were used. Observers performed 315 trials for each stimulus. Trial duration was 1500 ms plus response interval (unspeeded response).

Two observers participated in two additional control experiments. For the control experiment on detectability, procedure was modified as follows. Investigated phase angles were 0° and 90° for single-band stimulus and 45° and 22.5° for two-band stimulus. In the third of the trials, planar motion did not reverse (catch trials). Observers responded on using keys whether they saw no change in stimulus (*saw no change*), perceived the change but it was not accompanied by illusory motion reversal (*saw*
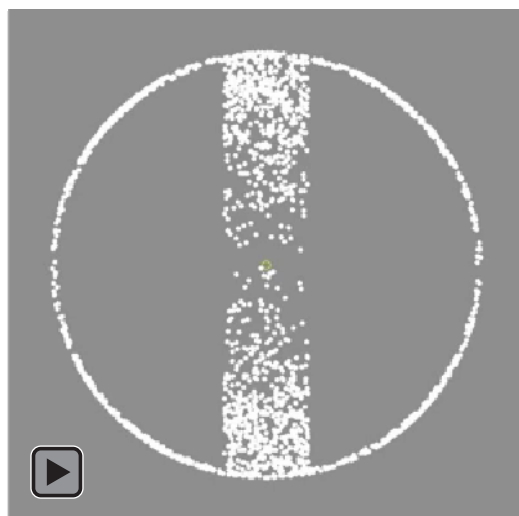


Movie 3. Two-band stimulus.
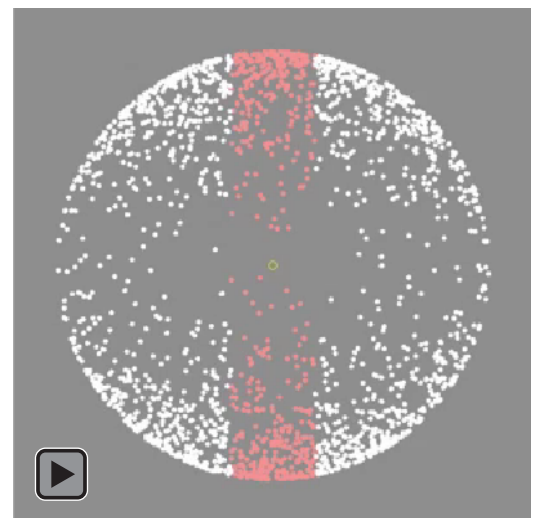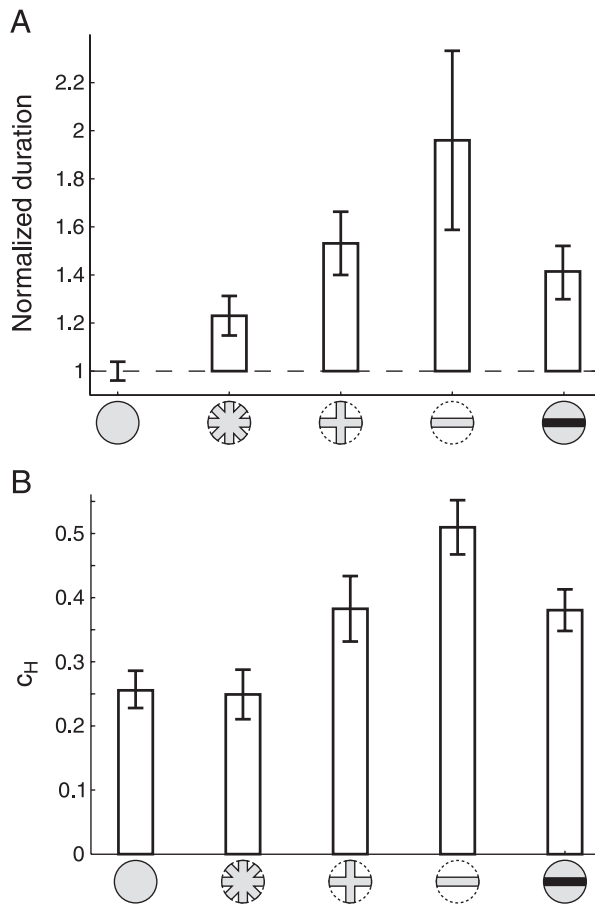


Movie 5. Colored-band stimulus.

Figure 4. Effect on perceptual dynamics. (A) Mean dominance duration for different displays, normalized to the mean dominance duration for uniform sphere. (B) Correlation with cumulative history for different displays (Pastukhov & Braun, 2011).

*change*), or saw an illusory motion reversal (*saw motion reversal*).

For the control experiment on effect of visual/motion transient, procedure was modified as follows. Investigated phase angles were 0° and 90° for single-band stimulus. Instead of planar motion inversion, all dots comprising the single-band display were randomly displaced to a new location. Observers responded the same way as in the main experiment.

## Experiment 3

Observers viewed a planar motion flow for 3000 ms through a mirror stereoscope. Each trial consisted of initial disambiguation period (300 ms), ambiguous (unperturbed) presentation (1200–1700 ms), stereoscopic depth period (200 ms), ambiguous (unperturbed) presentation (800–1300 ms), and response interval. Total trial duration was 3000 ms plus response interval (unspeeded response). Observers performed 255 trials for each stimulus.

During initial 300 ms, direction of rotation was disambiguated via stereoscopic depth cues and via continuous variations in dot size, with "front surface" dots being larger than "rear surface" dots (dot diameter from 0.2° to 0.05°). These measures induced the desired dominance state in 93% of all trials (failed trials were omitted from the analysis). At a random time between 1500 ms and 2000 ms, all dots acquired stereoscopic depth (while maintaining their size) for 200 ms, such that the stereoscopic depth of each dot was exactly opposite to its previous illusory depth (i.e., front dots were stereoscopically moved to the back and vice versa). The phase angle of the rotating volume was chosen such that the discontinuity was equally likely to occur at phase angles of 0°, 11.25°, 22.5°, …, 157.5°, and 168.75°. At the end of


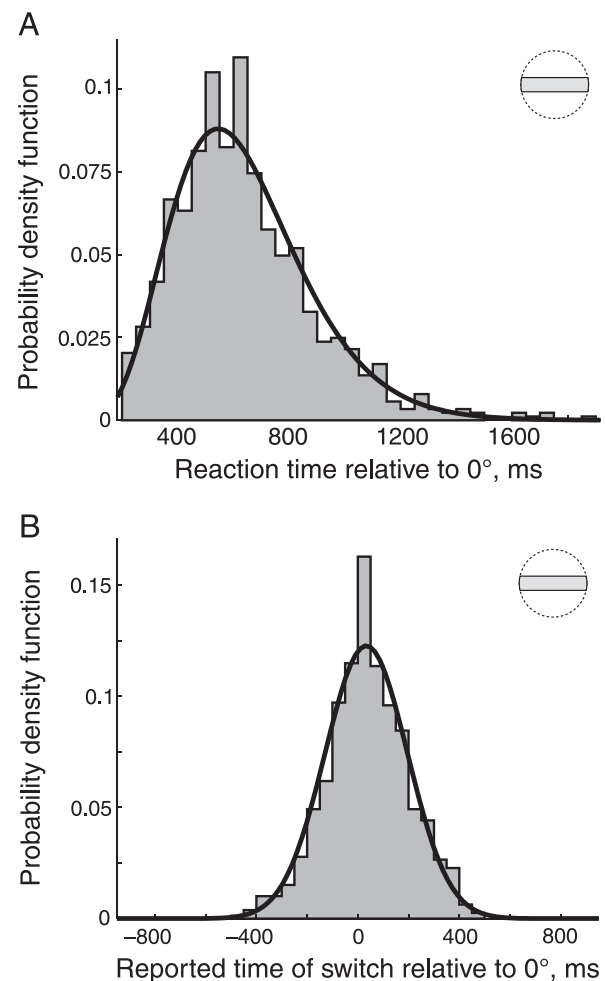
Figure 5. Different measures of reversal timing. Representative results for single-band display (Experiment 1). (A) Distribution of times of spontaneous reversal report, relative to moment of 0° phase angle, and fitted Gamma distribution (dark line). (B) Distribution of estimated reversal times using Libet dot, relative to moment of 0° phase angle, and fitted Gaussian distribution (dark line).
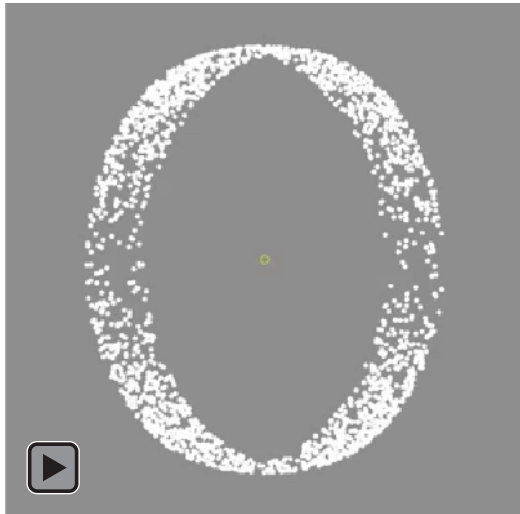
Movie 6. Experiment 2, Forced reversal of illusory depth of motion. Settings leading to illusory motion inversion outcome.

each presentation, observers reported the initial and final directions of perceived illusory rotation, using *arrow* keys. Only double-band and single-band stimuli were used.

# Results

## Experiment 1: Spontaneous reversal of illusory depth *and* motion

In order to explore how rotational asymmetry influences spontaneous perceptual alternations, we compared various shapes rotating about a vertical axis: bands, multiple bands, uniform spheres, and spheres with a color band, see Methods section and the illustrations and movies referenced therein. As all displays used in the study are dynamic, we strongly encourage readers to watch the supplied movies. Please ensure that movie presentation is looped.

The results are summarized by polar plots of the joint probability of reversing illusory depth and motion (Figure 6). Each plot shows the angular dependence as viewed from the axis of rotation. As expected, reversals of spheres showed no dependence on rotation angle (Figure 6A). However, already the reversals of four-band displays exhibited preferred angles spaced approximately 22.5° apart (Figure 6B). With the two-band display, the preference of certain rotation angles was more pronounced and the preferred angles were spaced approximately 45° apart (Figure 6C). Specifically, two-band displays reversed at rotation angles of 0°/90°/270°/180° (full frontal/edge on) and 45°/135°/225°/315° (diagonal). For

the single- and color-band displays, reversals occurred almost exclusively at rotation angles of 0°/180° (band fully frontal) and, much more rarely, at angles of 90°/270° (edge on; Figures 6D and 6E).

This pattern of results suggests that reversal probability is modulated by at least two angle-dependent factors. One of these factors is evidently depth symmetry (i.e., symmetry of the illusory volume to the frontal plane). Depth symmetry explains not only why single bands reverse only at two angles (frontal and edge on) but also why two bands reverse at four angles (also at diagonals) and why four bands reverse at eight angles. It is also consistent with previous studies that reported higher probability of spontaneous switches near angles of rotation that lead to depth symmetry (Brouwer & van Ee, 2006; Jackson et al., 2008; Wallach & O'Connell, 1953).

The second factor is more difficult to make out, but its existence is apparent from the results for one- and color-band displays: Reversals are far more likely at angles around 0°/180° (full frontal) than at angles around 90°/270° (edge on). Depth symmetry alone cannot account for this difference. To isolate and identify this second factor, we conducted two additional experiments.

## Experiment 2: Forced reversal of illusory depth *or* motion

As mentioned, spontaneous reversals involve simultaneous changes in the appearance of both illusory depth and motion. In order to dissociate these two aspects, we physically manipulated motion by inverting the direction
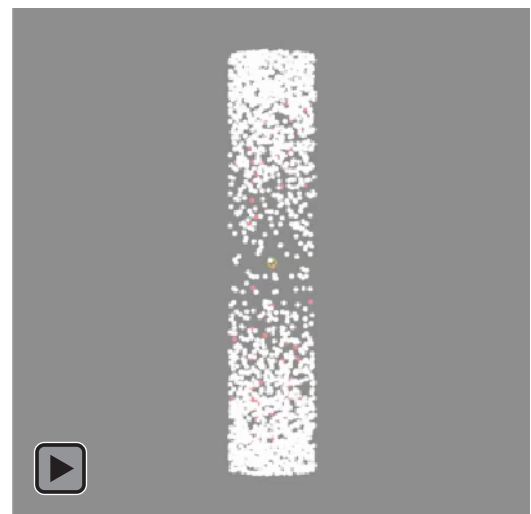


Movie 7. Experiment 2, Forced reversal of illusory depth of motion. Settings leading to illusory depth inversion outcome. Red dots were not present in the original display and were added only to make detection of depth reversal easier.
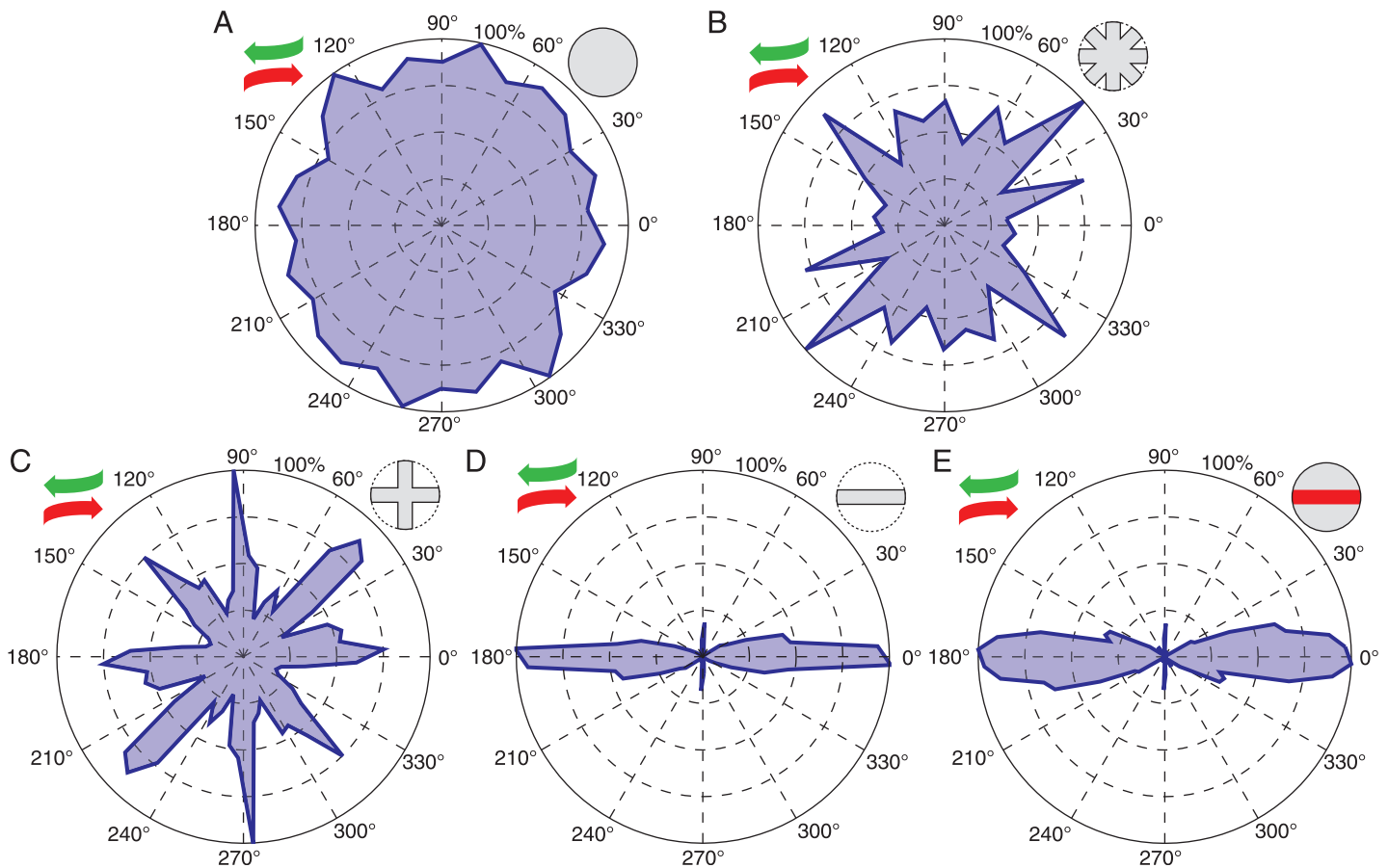
Figure 6. Spontaneous reversal of illusory depth and motion. Dependence of spontaneous reversal probability $p_{MD}(\alpha)$ on phase angle $\alpha$. Polar plots as viewed from axis of rotation. See also Figure 3 and Movies 1–5. (A) Uniform sphere. (B) Four bands. (C) Two bands. (D) Single band. (E) Color band.

of planar motion flow, thus creating an unstable perceptual state in which the illusory motion was no longer consistent with the illusory depth. In order to reestablish a consistent percept, the visual system had to respond by reversing *either* illusory motion *or* illusory depth. Thus, perception faced a "forced choice" and necessary had to alter one aspect (and only one aspect) of the illusory percept. Here, we investigated how often one alternative was chosen over the other, as a function of the rotational angle of the display. Note that this design reveals the relative probability of two alternative events, not the spontaneous rate of reversal events as the previous experiment.

Figure 7A illustrates the situation schematically for the single-band display (two-band displays were investigated as well, see also Movies 6 and 7). Initially, the display was perceived with a particular illusory motion (red arrow) and illusory depth (shading). At a particular angle of rotation (which was chosen by the experimenter), the planar motion was inverted (red arrow turns around and becomes green) and thus was no longer consistent with either the illusory motion or the illusory depth. The visual system then had two ways to reconcile the illusory percept

with the altered planar motion: It could reverse either the illusory motion or the illusory depth.

Phenomenally, the two reversal paths were quite distinct. A reversal of illusory rotation was a prominent event and was reliably reported by observers, even when the event itself had been missed (in which case the reversal could be detected by comparing current and remembered directions of rotation). In contrast, a reversal of illusory depth was less noticeable and could be perceived merely as a momentary "hesitation" in the illusory motion or even not at all. Observers reported whether or not they had perceived a change in illusory motion. As discussed above, the absence of such a change necessarily implied a change in illusory depth.

The results for single- and two-band displays are illustrated in Figures 7B and 7C. Polar plots show the relative probability of reversing illusory depth $p_D(\alpha)$ (as opposed to illusory motion), as a function of phase angle $\alpha$. Reversals of illusory depth occurred exclusively when the illusory shape was depth-symmetric, that is, for fully frontal, edge-on, and exactly diagonal (two-band only) viewing angles. This corroborates our earlier conclusion
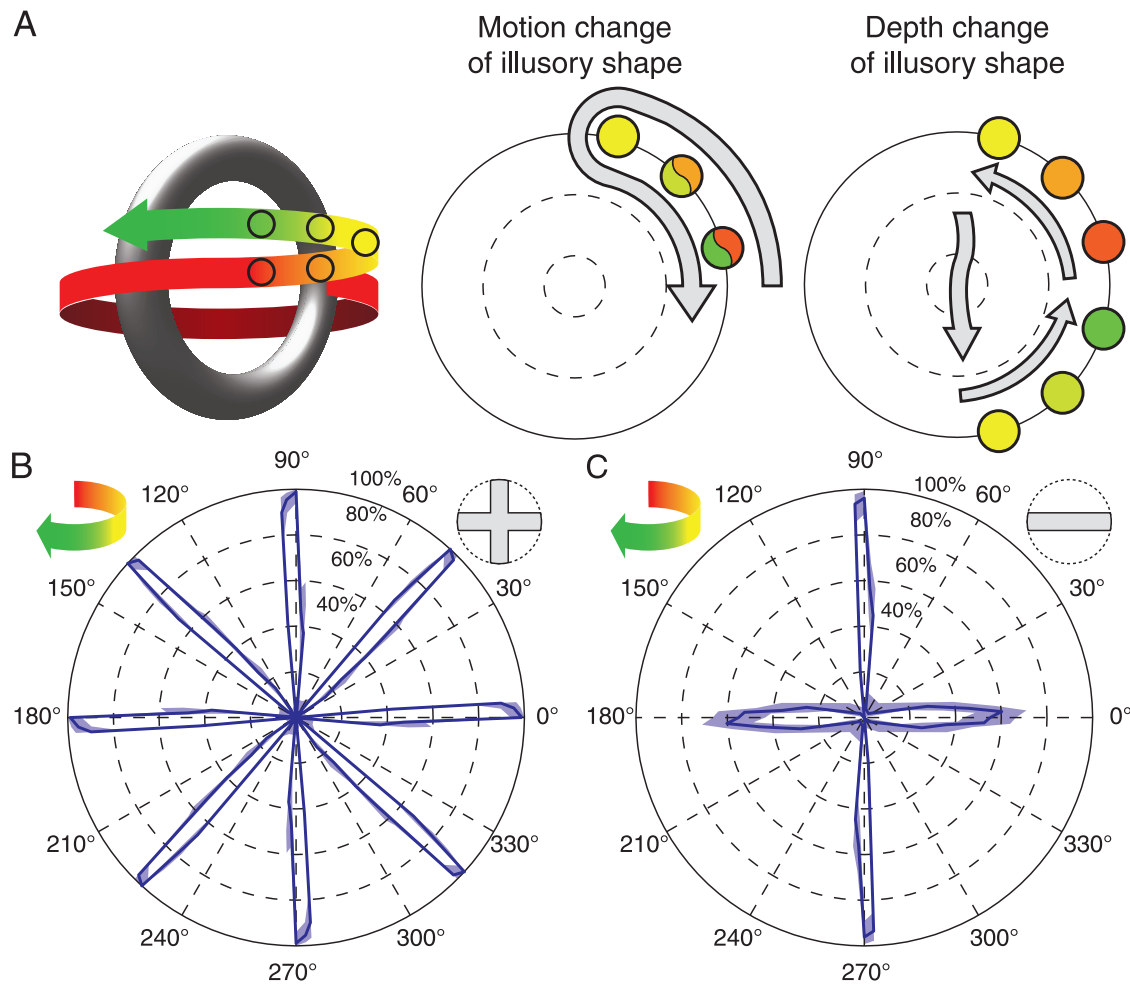
Figure 7. Forced reversal of illusory depth *or* motion. (A) Experimental design (schematic). An inversion of planar motion (left: frontal view, red arrow turns green) created an unstable situation, which was resolved by reversing either illusory motion (middle: axial view, dots retrace their steps) or illusory depth (right: axial view, dots invert in depth). Dot color indicates different stages during the inversion of planar motion. (B, C) Relative probability of depth reversal $p_D(\alpha)$ as a function of phase angle $\alpha$. Polar plots as viewed from axis of rotation. Mean and 95% confidence intervals of $p_D(\alpha)$ for (B) single-band display and (C) two-band display.

about depth symmetry as a necessary condition for depth reversals.

In contrast to Experiment 1, the single-band reversal probability was comparable at 0/180° and 90/270°. Presumably, this reflected the difference between forced and spontaneous reversals. In Experiment 2, a forced reversal was comparably likely to involve illusory depth during both frontal and edge-on views. In Experiment 1, spontaneous reversals were more likely to occur during frontal views.

The fact that reversals of illusory depth occurred only for depth-symmetric shapes also explains why these reversals were so unremarkable phenomenally as the perceived illusory shape and motion remained the same. Note, however, that a reversal of illusory depth was not a non-event: The assignment of individual dots to a depth plane, either at the front or the back of the illusory object, must necessarily have changed, even if the overall illusory shape

remained the same. To confirm that, we have performed a control experiment on the detectability of motion inversion at particular view angles, asking observers to report "motion reversal," "change," or "no change" in trials with a motion inversion or without it (catch trials). For the single-band stimulus, we have picked the 0° and 90° views, which result in depth symmetry. For two-band stimulus, we picked 45° view (maximal depth symmetry) and compared it with 22.5° view (minimal depth symmetry). Motion inversion was readily detectable at all viewing angles, except the 0° angle of the single-band display Table 1). In this one exceptional case, the extreme foreshortening renders individual dots virtually indistinguishable.

As we have explained above, inversion of planar flow creates an unstable perceptual state; however, it also introduces a motion transient. We have performed a control experiment to examine whether results of Experiment 2 can be reproduced with motion transient alone. To this

| | | Report | | |
|---|---|---|---|---|
| Stimulus | Angle of reversal | Saw no change | Saw change | Saw motion reversal |
| Single-band | 0° | 65% | 3% | 32% |
| | 90° | 4% | 93% | 3% |
| | Catch trial | 98% | 2% | 0% |
| Two-band | 45° | 8.8% | 89.5% | 1.7% |
| | 22.5° | 0% | 1% | 99% |
| | Catch trial | 100% | 0% | 0% |

Table 1. Detectability of planar flow inversion at particular view angles for single- and two-band stimuli.

end, we have displaced all dots comprising a single-band display at 0° or 90° of rotation. We find displacement to be a weaker manipulation: It prompted reversal of illusory motion in only 3% of trials for both angles of rotation, compared to 15.4% and 32% following the motion inversion. Accordingly, visual and/or motion transient alone is insufficient to explain the results of Experiment 2.

## Experiment 3: Induced reversal of illusory motion

In our third experiment, we destabilized perception by manipulating stereoscopic depth. Specifically, we transiently inverted the illusory depth by adding opposite stereoscopic depth. After the stereoscopic transient, perception could stabilize the inverted depth, in which case it also had to reverse the illusory motion. Alternatively, the transient could be ignored and perception could continue with the original illusory depth and motion. Once again, we investigated how often the visual system chooses one alternative over the other as a function of the rotational angle of the display.

Figure 8A illustrates the situation schematically for the single-band display (two-band displays were studied as well). Initially, the display was perceived with a particular illusory motion (red arrow) and illusory depth (shading). At a particular angle of rotation, stereoscopic depth was added to all dots for a period of 200 ms. This stereoscopic depth was always *opposite* to the perceived illusory depth, thus inverting the latter. With depth transiently inverted, the further evolution largely reflected the ease (or difficulty) of reversing illusory motion. If motion reversed as well, the transition between illusory percepts was complete. If motion failed to reverse, the illusory percept remained unchanged. Phenomenally, the two reversal paths were again distinct: A completed reversal of illusory rotation was phenomenally prominent, while an abortive reversal appeared (at best) as a momentary "fuzziness" in the display.

The results for single- and two-band displays are illustrated in Figures 8B and 8C. Polar plots show the probability of reversing illusory motion $p_M(\alpha)$ (completed transition of illusory percept), as a function of phase angle $\alpha$. The probability of motion reversals exhibits a moderate dependency on phase angle but remains finite at

all angles (i.e., there are no "forbidden" angles). For one-band displays, this probability is maximal near 0°/180° and minimal near 90°/270°. For two-band displays, it is maximal near diagonal view angles (45°/135°/225°/315°) and minimal near axial view angles (0°/90°/270°/180°).

Reversals of illusory motion did not depend on depth symmetry in the way depth reversals did. Neither did they depend on the amplitude of the disparity transient. The probability of motion reversals was smallest when the disparity transient was largest (90°/270°) and largest when the disparity transient was smallest (0°/180°). This implies that the disparity transient effectively destabilized illusory depth at all phase angles.

We hypothesize that the probability of motion reversals varies with the average speed of planar motion: the faster the planar motion, the smaller the reversal probability. This would be consistent with the extensive prior evidence about the illusory appearance of depth from motion being predicated on relative speed (Nawrot & Blake, 1991; Sperling & Dosher, 1994).

An alternative explanation can be that more gradual dependence is due to slower processing of stereoscopic depth (Uomori & Nishida, 1994). If the difference would lie in the speed with which the two manipulations take effect, then the probability peaks observed when inverting planar motion should be delayed and broadened when inverting stereoscopic depth. However, this is not the case: For the single-band stimulus, four probability maxima and four minima in Experiment 2 become two maxima and two minima in Experiment 3. For the two-band stimulus, eight maxima and minima become four maxima and minima. In addition, we would point out that probability maxima and minima for reversals induced by stereoscopic depth are perfectly in phase with particular views (representing maxima and minima of planar motion speed). If the effectiveness of the stereoscopic manipulation had been delayed appreciably, there would have been some phase shift. Accordingly, we can confidently rule out a delayed effect.

## Quantitative comparison

The preceding experiments established the reversal probabilities of illusory motion and depth as a function
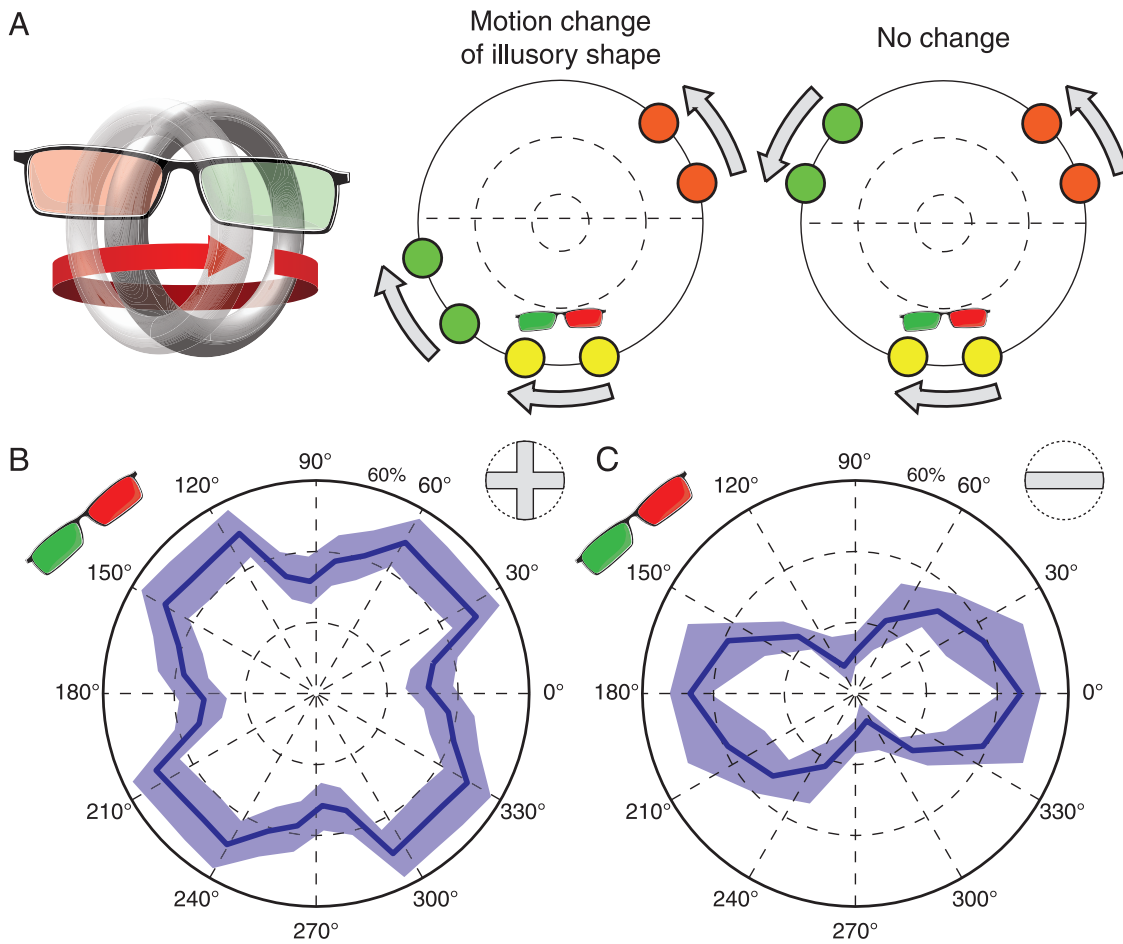
Figure 8. Induced reversal of illusory motion. (A) Experimental design (schematic). An inversion of illusory depth using stereoscopic cues (left: frontal view, inverted shading) created an unstable situation, which was resolved either by an additional reversal of illusory motion (middle: axial view, dots move "ccw," invert in depth, and invert motion to "cw") or by a return to the initial illusory percept (right: axial view, dots move "ccw," transiently invert in depth, but continue with "ccw" motion). Dot color indicates different stages before (red), during (yellow), and after (green) the inversion of depth. (B, C) Probability of motion reversal $p_{M}(\alpha)$ as a function of phase angle $\alpha$. Polar plots as viewed from axis of rotation. Mean and 95% confidence intervals of $p_{M}(\alpha)$ for (B) single-band display and (C) two-band display.

of phase angle $\alpha$. Experiment 1 established the joint probability of spontaneous reversals of illusory motion *and* depth, $P_{MD}(\alpha)$. Experiment 2 measured the individual probability of a reversal of illusory depth $P_{D}(\alpha)$, and Experiment 3 revealed the individual probability of a reversal of illusory motion $P_{M}(\alpha)$.

Due to differences in experimental protocols, the absolute reversal rates could not be compared meaningfully. Accordingly, it was convenient to distinguish angular dependencies from the maximal rates:

$$
\begin{aligned}
P_{MD}(\alpha) &= \rho_{MD}p_{MD}(\alpha), \\
P_{D}(\alpha) &= \rho_{D}p_{D}(\alpha), \\
P_{M}(\alpha) &= \rho_{M}p_{M}(\alpha),
\end{aligned}
\qquad (1)
$$

where $\rho_{MD}$, $\rho_{D}$, and $\rho_{M}$ are the maximal rates and $p_{MD}(\alpha)$, $p_{D}(\alpha)$, and $p_{M}(\alpha)$ are the observed angular dependencies.

To approximate the effect of depth symmetry, we computed for each rotation angle the average *minimal*

distance $D(\alpha)$ over all pairs of left- and right-moving dots and use this measure as a "penalty" in an exponential function $f(\alpha)$:

$$
p_{D}(\alpha) \approx f_{D}(\alpha), \ f_{D}(\alpha) \equiv a \cdot \exp\left(-\frac{D^{2}(\alpha)}{\kappa}\right),
\qquad (2)
$$

where $a$ and $\kappa$ are constants. To fit results of Experiment 2, we subtracted $f_{D}(\alpha)$ from the observed function $p_{M}(\alpha)$ of Experiment 3. The best (least-squares) fit of $p_{M}(\alpha) - f_{D}(\alpha)$ to the observed function $p_{D}(\alpha)$ of Experiment 2 was obtained with $a = 3.2$ and $\kappa = 0.03$ (Figure 9A).

To approximate the effect of planar speed, we computed the average absolute value of the cosine of the rotation angle $\beta_{i}$ of all dots $i$ and use this measure as a "penalty" in a linear function $f_{M}(\alpha)$:

$$
p_{M}(\alpha) \approx f_{M}(\alpha), \ f_{M}(\alpha) \equiv \frac{1}{M}\sum_{i=1}^{M}|\cos(\beta_{i})|,
\qquad (3)
$$
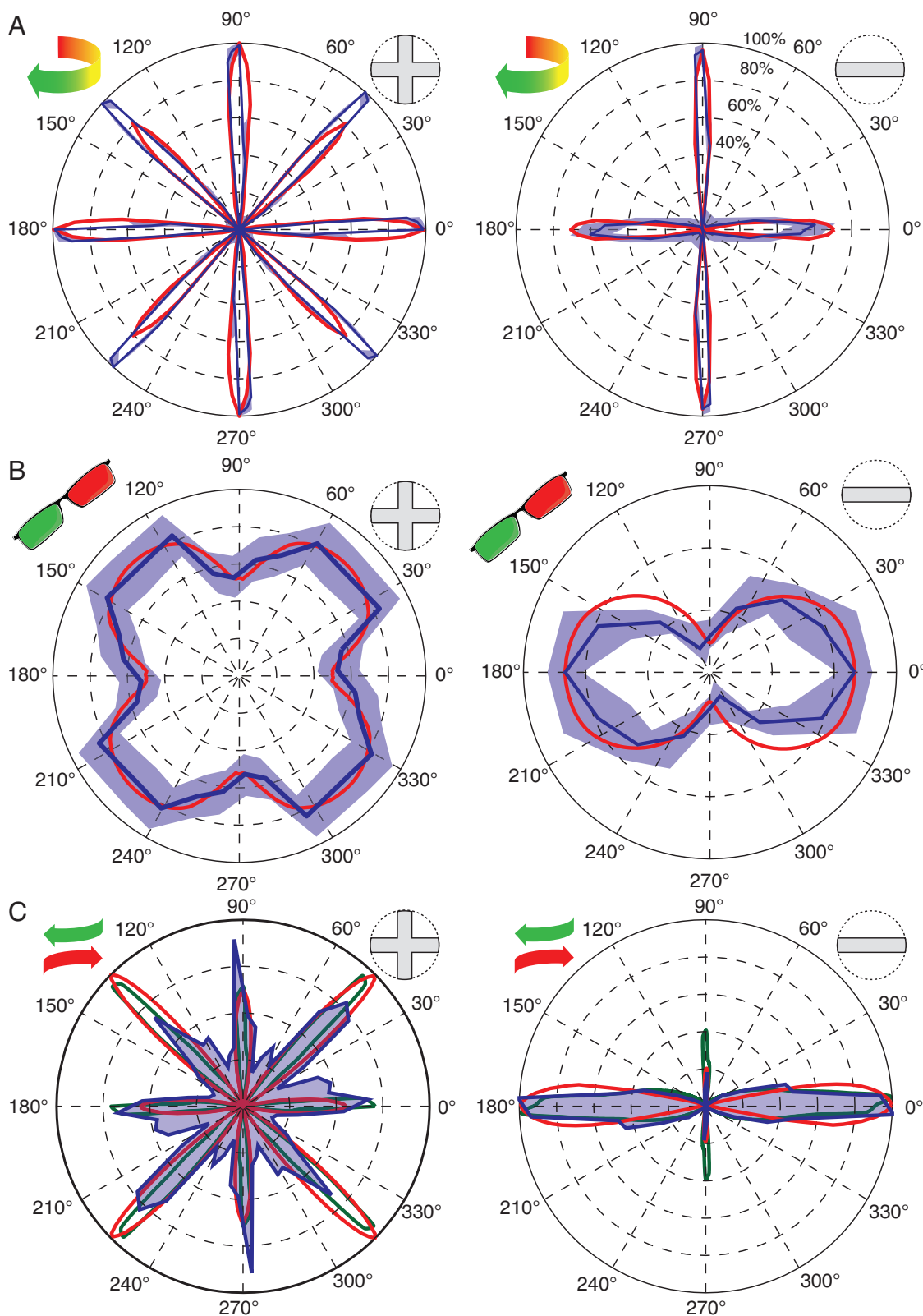
Figure 9. Model fits. Blue curves and areas represent experimental observations $p_D$, $p_M$, and $p_{MD}$ (mean ± standard error). Red curves represent model fits $f_D$, $f_M$, and $f_M f_D$. Green curves represent the product $p_M p_D$. The results from two-band displays (left column) and single-band displays (right column) are shown. (A) Comparison of $p_D$ and $f_D$. (B) Comparison of $p_M$ and $f_M$. (C) Three-way comparison of $p_{MD}$, $p_M p_D$, and $f_M f_D$.

Movie 8. Bi-stable but slow switching stimulus.

where $|x|$ is the absolute value of $x$. The sum includes all dots except near stationary ones (planar speed below 0.12°/s; Figure 9B).

Interestingly, the probability of a spontaneous joint reversal of motion and depth (Experiment 1) was well approximated by the product of the individual probabilities of reversing either depth alone (Experiment 2) or motion alone (Experiment 3). This is illustrated in Figure 9C, which compares the observed function $p_{MD}(\alpha)$ with the products $p_M(\alpha)p_D(\alpha)$ and $f_M(\alpha)f_D(\alpha)$. Thus, the independence assumption

$$p_{MD}(\alpha) = p_M(\alpha)p_D(\alpha), \qquad (4)$$

provides an excellent fit and captures most the variance, $R^2 = 0.72$.

To test the generality of these results, we sought to devise uncommonly stable depth-from-motion displays. We surmised that the illusory shape should be highly stable when it is never depth-symmetric and when planar differentials are always high. Numerous shapes satisfy these constraints, including the well-known "rotating ballerina" (http://www.procreo.jp/labo/silhouette.swf) and the shape in Movie 8. Average dominance times for the latter shape were approximately 30 times longer than for spherical shapes ($142 \pm 20$ s compared to $4.8 \pm 0.5$ s, 3 observers).

# Discussion

In three experiments, we have shown that the reversal probability of rotating illusory volumes varies dramatically with phase angle. As depth-from-motion displays are uniformly ambiguous, they support two equally plausible alternative percepts at every phase angle. It follows that the observed dependence on phase angles cannot be due to differences in the relative stability of alternative percepts. Instead, it must reflect differential availability of "transitional paths" between percepts.

Specifically, the respective probabilities of depth and of motion reversals exhibit separate and independent dependencies on phase angle. While depth reversals of an illusory shape depend on depth symmetry (in an all-or-nothing fashion), motion reversals depend on planar motion speed (in a graded fashion). Combined reversals of both depth and motion exhibit a more complex dependency, which is well approximated by the product of the individual dependencies (Figure 9C). In other words, at any given phase angle, the probability of a joint reversal is well approximated by the product of the probabilities of individual reversals. This implies that reversals of illusory depth and illusory motion behave as independent random processes.

Qualitatively, our results are consistent with two independent energy landscapes governing reversals of illusory depth and motion (Figure 10). For illusory depth, the transition energy is either zero (for frontally symmetric shapes) or high (for all others). In contrast, the transition energy for illusory motion varies smoothly with input strength (speed of planar motion). A combined reversal of both depth and motion (i.e., a spontaneous reversal) requires transitions in both landscape and, thus, the sum of the two individual transition energies. The observed multiplicative behavior of transition probabilities can be understood if each probability exhibits a Boltzman-like dependence on transition energy.

What could be the reason for the angle dependence of "transitional paths"? What could prevent the transition to an equally plausible illusory shape? Why would the "end" (plausible illusory shape) not always justify the "means" (transitional path)? The most likely answer lies in ecological validity of the involved transformations. Visual perception is the outcome of an inferential process, which combines the current retinal evidence with prior experience of the visual world (Gerardin, Kourtzi, & Mamassian, 2010; Gregory, 1997; Kersten, Mamassian, & Yuille, 2004; Weiss, Simoncelli, & Adelson, 2002; Yang & Purves, 2003). The illusory appearance of depth-from-motion displays exemplifies this tendency to extrapolate beyond the evidence particularly well. We hypothesize that prior experience shapes not merely the illusory volumes but also the "transitional paths" between such volumes. Specifically, the visual world offers numerous examples of rotating objects suddenly reversing their rotation (e.g., due to an impact or a collision). In contrast, it is difficult to conceive of any circumstances in which a solid object would reverse in depth (i.e., be transformed into its mirror image with respect to the frontal plane). In short, we surmise that reversals of illusory motion take place, because there are precedents for such events in the
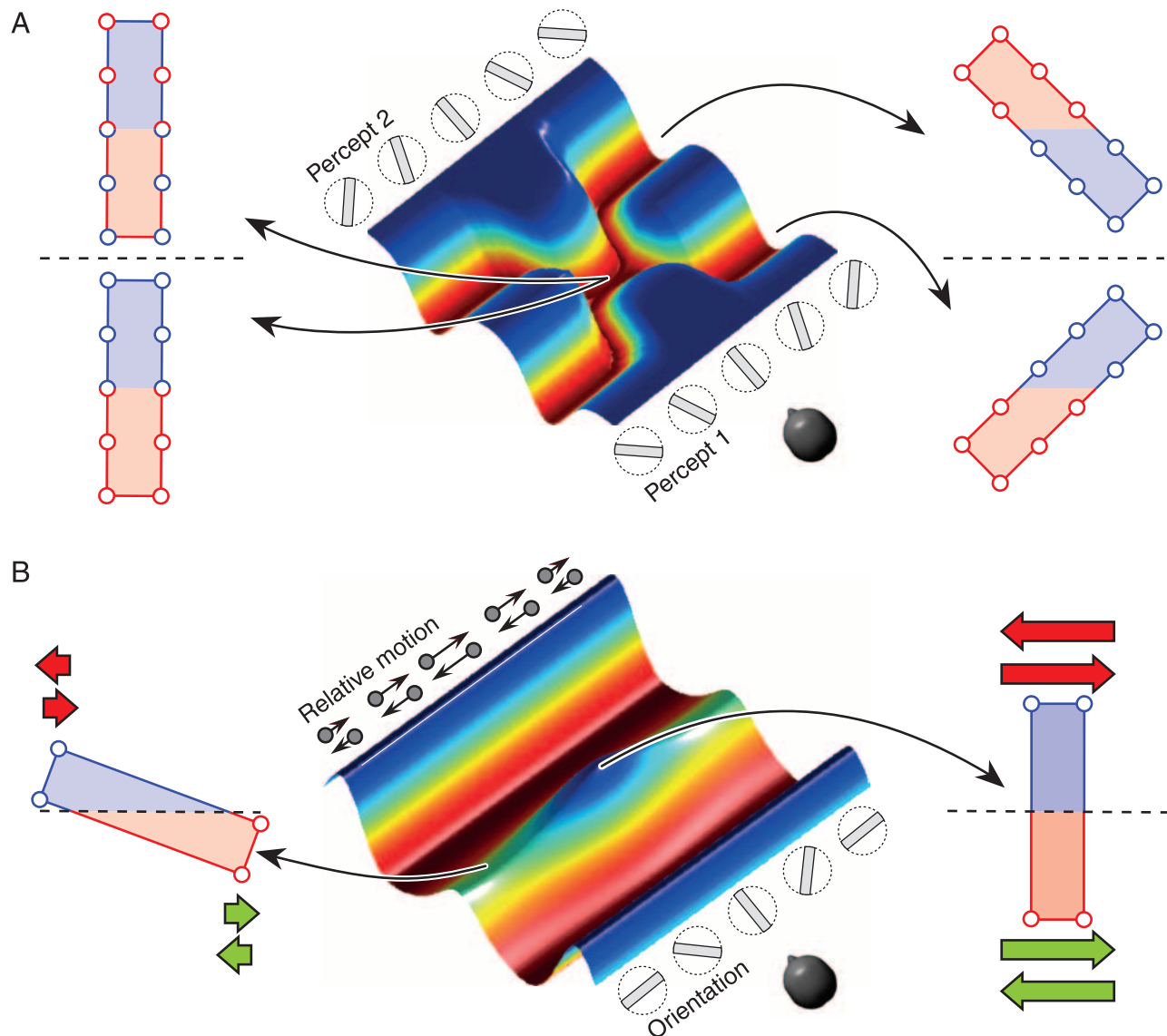
Figure 10. Qualitatively different energy landscapes govern transitions of illusory depth and motion (schematic). Our results are consistent with two energy landscapes that independently govern transitions of illusory depth and motion. Spontaneous reversals of illusory shape link both transitions. (A) The transition energy for illusory depth is either zero (left: frontally symmetric shapes) or high (right: all others), reflecting the physical implausibility of spontaneous inversions in depth. (B) In marked contrast, the transition energy for illusory motion varies smoothly with planar motion speeds, being smaller for low speeds (left) and larger for high speeds (right). This may reflect the comparative physical plausibility of spontaneous inversions in the direction of rotation.

visual world, whereas reversals of illusory depth do not occur, because there are no precedents for such events.

At this point, the reader may object that reversals of illusory depth did occur at least for depth-symmetric shapes. However, such reversals evidently did not involve any change in the perceived illusory shape. Consider the single-band stimulus illustrated in Figure 10. While the band is oriented between 0° and 90°, any depth reversal would imply a change in the illusory shape (right inset). However, at the two points of depth symmetry (0° and 90°), a depth reversal leaves the overall shape of the illusory volume unchanged (left inset). The only change is the assignment of individual dots to the front and back

halves of this volume. In other words, a reversal of illusory depth does not involve any change in the illusory shape but merely a reassignment (or "rebinding") in the illusory depth and motion of individual stimulus dots.

The hypothesis here advanced—that prior experience restricts the perception of shape transformations—is well supported by earlier findings (Tse, 2006; Tse, Cavanagh, & Nakayama, 1998; Tse & Logothetis, 2002). When one shape is replaced by another, observers often perceive an (illusory) transformation (e.g., shooting line effect). The relevance of this in the present context is that observers tend to perceive one particular transformational path and not any of the many other possible paths ("transformational

apparent motion" or "TAM"; Tse & Logothetis, 2002). Just like in TAM, fate of the object is ambiguous and validity of transformation has to be known before matching or maintaining figural identity across successive scenes can be attempted. This shows that visual inference is guided (at least in part) by priors about transformational paths. Evidently, shape perception is constrained not merely by current information but also by the presumed continuity with shapes perceived previously at the same location. The advantage of relying on this additional information (i.e., temporal context) is evident.

We have presented evidence that the spontaneous transformations of perceived shape in depth-from-motion displays are guided by prior experience of transformational paths in the visual world. In this respect, illusory shapes are constrained just as much by temporal context as are any other shapes perceived in unambiguous visual scenes. In addition, we have shown that spontaneous transformations of perceived shape involve two independent random processes, namely, reversals of illusory motion and reversals in the "assignment" of illusory depth.

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