

Exogenously triggered perceptual switches in multistable structure-from-motion occur in the absence of visual awareness

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Here, we characterize the duration of exogenously triggered perceptual switches in an ambiguously rotating structure-from-motion display and demonstrate their independence on visual awareness. To this end, we triggered a perceptual reversal by inverting the on-screen motion and systematically varied the posttrigger presentation duration, while collecting observers' reports about the initial and final directions of illusory rotation. We demonstrate that for the structure-from-motion display, perceptual transitions are extremely brief (≤ 20 ms) and can be considered instantaneous from an experimental perspective. We also report that although very brief posttrigger intervals (10–20 ms) reliably initiate a perceptual reversal, observers become aware of perceptual switches only if the posttrigger presentation continues for at least 80 ms. Additional experiments demonstrated that an observed lack of visual awareness for brief posttrigger presentation intervals cannot be attributed to either a systematic delay of visual awareness or to backward masking. Our results show that exogenously triggered perceptual reversal can occur in the absence of visual awareness, extending earlier work on spontaneous reversals that indicated that neither awareness nor attention may be required for multistable perception. Methodologically, the brevity and the short latency of induced perceptual reversals make them particularly suitable for finely timed experiments, such as magneto/electroencephalography studies.

Introduction

Typically, we experience our perception as stable and unambiguous, in a sense that the same retinal input results in the same perception that remains constant even during prolonged viewing. However, this seeming one-to-one relationship between sensory inputs and perception is an illusion (Gregory, 2009; Metzger, 2009). This is particularly clear when it is violated by so-called multistable displays that are compatible with several distinct and comparably plausible perceptual interpretations. These displays force the visual perception to continuously switch between alternatives despite constant sensory evidence (Blake & Logothetis, 2002; Leopold & Logothetis, 1999).

The single most studied aspect of multistable perception is perceptual switching, and we have a fair, although hardly complete, understanding of how the occurrence of perceptual reversals can be predicted from the stimulus properties (Brouwer & van Ee, 2006; Kang, 2009; Levelt, 1965) and prior perceptual experience (Blake, Westendorf, & Fox, 1990; Kang & Blake, 2010; Nawrot & Blake, 1989; Pastukhov & Braun, 2011; Wolfe, 1984). The neural correlates of endogenous triggers of spontaneous reversals are currently debated, but recent evidence from imaging

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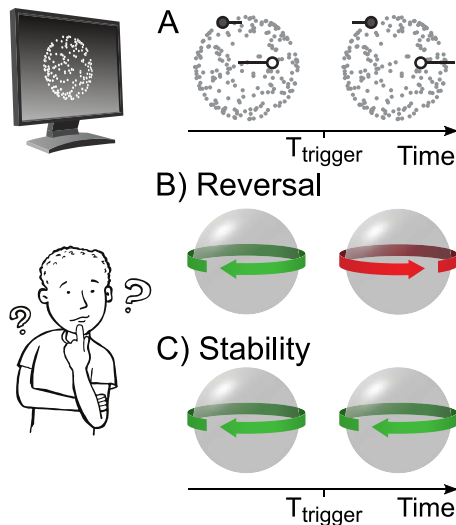


Figure 1. An exogenously triggered reversal of illusory rotation in structure-from-motion displays. Either an inversion of the 2D motion at time T_{trigger} (A, illustrated for two example dots) may trigger a reversal of the illusory rotation (B) or the illusory rotation may remain stable, following a spatial readjustment of individual flow elements (C). See also Movie 1.

studies suggests that they are localized in sensory areas of the brain rather than in regions associated with executive control and attention (Frässle, Sommer, Jansen, Naber, & Einhäuser, 2014; Knapen, Brascamp, Pearson, van Ee, & Blake, 2011; Weilhhammer, Ludwig, Hesselmann, & Sterzer, 2013). Less is known about the duration of perceptual reversals and about the exact temporal relationship between a trigger event, changes within a sensory representation, and the following visual awareness of that switch. This is primarily because we infer the timing of perceptual reversals from observers' immediate responses, which are too variable to provide a reliable estimate (Pastukhov, Vonau, & Braun, 2012).

To overcome this limitation, we investigated the temporal characteristics of *exogenously* triggered switches (Pastukhov et al., 2012; Treue, Andersen, Ando, & Hildreth, 1995; see Figure 1; Movie 1). To quantify the duration of exogenously triggered perceptual switches in structure-from-motion (SFM) displays, we established the duration of the intermediate/mixed perception following an exogenous trigger event. For this, we report that perceptual reversals in SFM are extremely brief. In addition, we combined several experimental measures to dissociate a dominance change within sensory representations and the visual awareness of this change. We demonstrate that although the inversion of the on-screen motion appears to trigger the reversal of perceptual dominance even if the posttrigger presentation is stopped after 20 ms, the observers become aware of that only if the following presentation period is at least 80 ms long. In other

words, exogenously triggered perceptual reversals occur in the absence of visual awareness.

Methods

Observers

Procedures were in accordance with the Declaration of Helsinki and were approved by the medical ethics board of the Otto-von-Guericke Universität, Magdeburg: "Ethik-Kommission der Otto-von-Guericke-Universität an der Medizinischen Fakultät." All participants had normal or corrected-to-normal vision. Apart from the second author, observers were naive to the purpose of experiments and were paid for their participation.

Apparatus

Stimuli were generated with MATLAB using the Psychophysics Toolbox (Brainard, 1997) and displayed on a CRT screen (Iiyama VisionMaster Pro 514, iiyama.com, resolution $1,600 \times 1,200$ pixels, refresh rate 100 Hz). The viewing distance was 73 cm so that each pixel subtended approximately 0.019° . Observers responded using a keyboard. Background luminance was kept at 36 cd/m^2 . The experimental room was lit dimly (ambient luminance at 80 cd/m^2).

Display

The SFM stimulus consisted of 50 dots distributed over the surface of the sphere. The sphere diameter was 5.7° , and the dot diameter was 0.057° . For the *main* object (presented during the main T_{on} interval), the dots were distributed in such a way as to ensure a specific distance between all left- and right-moving dots at the time of the on-screen motion inversion (T_{trigger} , offset of $T_{\text{pre/onset}}$ of T_{post} presentation intervals) to maximize the probability of triggering a perceptual switch (see Stonkute, Braun, & Pastukhov, 2012, for details). For the *probe* stimulus (presented during the probe interval), the dots were distributed randomly over the surface of the sphere. Both main and probe stimuli were generated anew on every trial.

Experiment 1

Nine observers (five of them female, four male) participated in the experiment. Each of the four experimental conditions (see below) was measured in a separate experimental session. Each session consisted

of eight blocks, and each block contained 70 trials. Note that the trials from Experiments 1 and 2 were equally intermixed during each block (i.e., 35 trials belonged to Experiment 1 and 35 to Experiment 2).

Each trial consisted of a random onset delay (0.5–1 s), a pretrigger interval ($T_{\text{pre}} = [500, 625, 750, 875, 1000]$ ms), an *optional* posttrigger interval ($T_{\text{post}} = [10, 20, 40, 80, 160, 320]$ ms), and a response interval (Figure 2A). The direction of the two-dimensional (2D) motion was inversed at the onset of the posttrigger interval, and the presentation continued for a predefined amount of time (T_{post}). The purpose of the on-screen motion inversion was to trigger a reversal of the perceived illusory rotation (Pastukhov et al., 2012; Treue et al., 1995; see Figure 1). The “no inversion” presentation condition contained no on-screen motion inversion and, correspondingly, no postinversion presentation interval (Figure 2B).

The dots were distributed on the surface of the illusory sphere in such a way as to ensure a specific minimal distance between pairs of left- and right-moving dots at the time of the on-screen motion inversion (Stonkute et al., 2012). We used four interpair distances to systematically manipulate the strength of the motion transient and, therefore, the probability of successfully induced perceptual reversals. The four conditions were labeled according to the strength of the motion transient: *Strong (1)/S1*, *Strong (2)/S2*, *Medium/M*, and *Weak/W*. The maximal induced destabilization was determined using the longest post-trigger interval duration ($T_{\text{post}} = 320$ ms; for further details, see the Results sections for Experiments 1 and 2). Please note that the effectiveness of the motion transient in inducing a perceptual reversal depends not only on its strength but also on a prior perceptual history (Pastukhov, Vivian-Griffiths, & Braun, 2015). The same procedure but using variable *pretrigger* intervals has been used to study the onset perception of SFM displays (Pastukhov, 2015).

Observers reported on initial (beginning of T_{pre} , labeled as R(1)) and final (end of T_{post} interval or end of T_{pre} interval for “no inversion” condition, labeled as R(2)) directions of illusory rotation. Observers had an option of reporting an unclear/mixed percept via the “down” key. The response times were measured with respect to the end of the presentation (offset of T_{post} or T_{pre} for “no inversion” condition). Accordingly, perceptual destabilization due to an endogenous trigger event was quantified as

$$P_{\text{reversal}} = P(R(1) \neq R(2)). \quad (1)$$

Group averages were fitted with a logistic function using the Palamedes toolbox (Prins & Kingdom, 2009). Standard errors of measurement for the free parameters

of the logistic function were obtained using a bootstrap procedure implemented in the Palamedes toolbox.

Experiment 2

Nine observers (five female, four male) participated in the experiment. The procedure was identical to that of Experiment 1 but for an additional probe SFM display. The visual sequence of Experiment 1 was followed by a brief blank interval ($T_{\text{blank}} = 50$ ms) and the probe SFM display ($T_{\text{probe}} = 500$ ms). The probe stimulus was a *different* sphere (i.e., the location of individual flow elements was different from that of the main sphere). Observers reported on the initial rotation of the main stimulus and on the final direction of illusory rotation of the probe display. See Figure 3A. Note that trials from Experiments 1 and 2 were equally intermixed during each block (i.e., 35 trials belonged to Experiment 1 and 35 to Experiment 2).

Experiment 3

Six observers (three of female, three male) participated in the experiment. The SFM display was identical to the *Strong (1)/S1* condition of Experiments 1 and 2. The presentation schedule of the SFM display was similar to that of Experiments 1 and 2 but without the “no inversion” condition and with only long post-trigger intervals ($T_{\text{post}} = [140, 150, 160, 170, 180]$ ms). The SFM display was accompanied by a yellow dot (diameter 0.75°) that moved clockwise along the circular trajectory (radius 5.7°) with a speed of $600^\circ/\text{s}$. The initial position of the dot was randomized. Please see Movie 2, which demonstrates several presentation trials without a response interval (please note that the actual experimental display looked different because of a higher refresh rate). After the presentation, the SFM display was taken of the screen, and the dot was moved to a random location that was at least 45° away from the location the dot was in at the time of the on-screen motion reversal. The observers were instructed to memorize the location of the yellow dot at the time of the illusory rotation reversal. They used arrow keys (left and right) to move the dot to the memorized location and “Enter” to confirm it. Observers had an option to report the lack of reversal using a “Q” key ($11.6\% \pm 12.7\%$ of trials).

Experiment 4

Seven observers (four female, three male) participated in the experiment. Apart from an added 500-ms delay before the response prompt, the procedure was

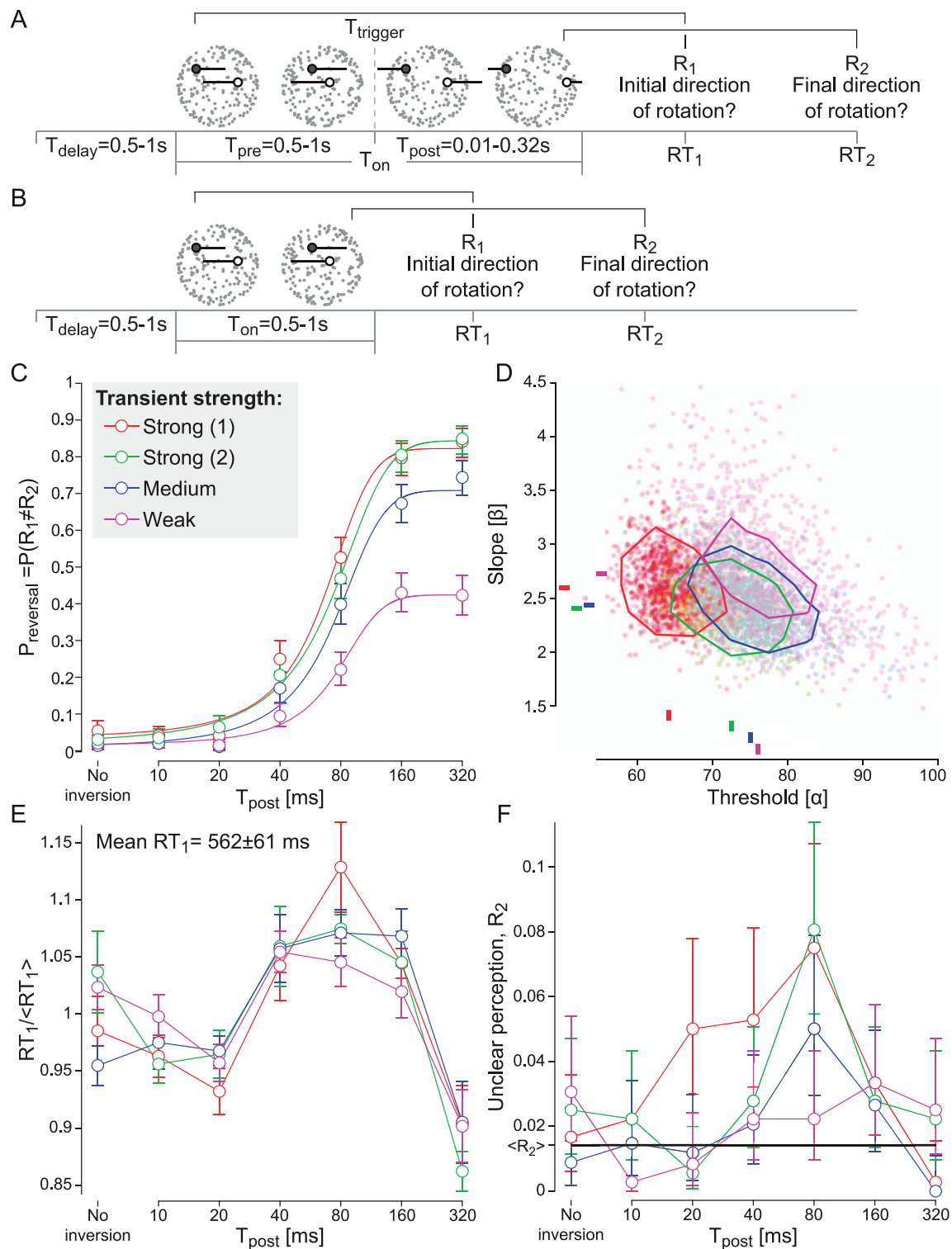


Figure 2. Experiment 1. (A) Schematic procedure. Each trial consisted of a random-onset delay ($T_{\text{delay}} = 0.5-1\text{ s}$), a presentation interval ($T_{\text{on}} = T_{\text{pre}} + T_{\text{post}}$), and a response interval. The direction of the on-screen motion was inverted at the end of the T_{pre} interval, and the presentation continued for a predefined amount of time (T_{post}). The purpose of the on-screen motion inversion was to trigger a reversal of the perceived illusory rotation. Observers reported on the initial (R_1) and final (R_2) directions of illusory rotation. (B) Schematic procedure for the "no inversion" presentation condition. The procedure was similar but for the omitted on-screen motion inversion and the lack of the posttrigger interval. (C) Probability of reversal as a function of the posttrigger interval duration T_{post} (mean and 95% confidence interval based on binomial distribution). Curves depict best-fitting logistic functions. (D) Distributions of slope and threshold. (E) Ratio of RT_1 to $RT_1 >$ as a function of the posttrigger interval duration T_{post} . The mean $RT_1 = 562 \pm 61\text{ ms}$. (F) Unclear perception, R_2 as a function of the posttrigger interval duration T_{post} . A horizontal line is drawn at $\langle R_2 \rangle \approx 0.015$.

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threshold (α) and slope (β) parameters obtained by parametric bootstrapping (1,000 iterations). Solid curves encircle 68.27% of the data points. Bars depict the mean and standard error for each distribution and parameter. (E) Normalized response time for the initial direction of rotation (RT_1) as a function of the posttrigger interval duration (T_{post}). Gray stripe: SEM for an overall average. (F) Fraction of “unclear” responses for the final direction of rotation (R_2) as a function of the posttrigger interval duration (T_{post}). Gray stripe: SEM for an overall average.

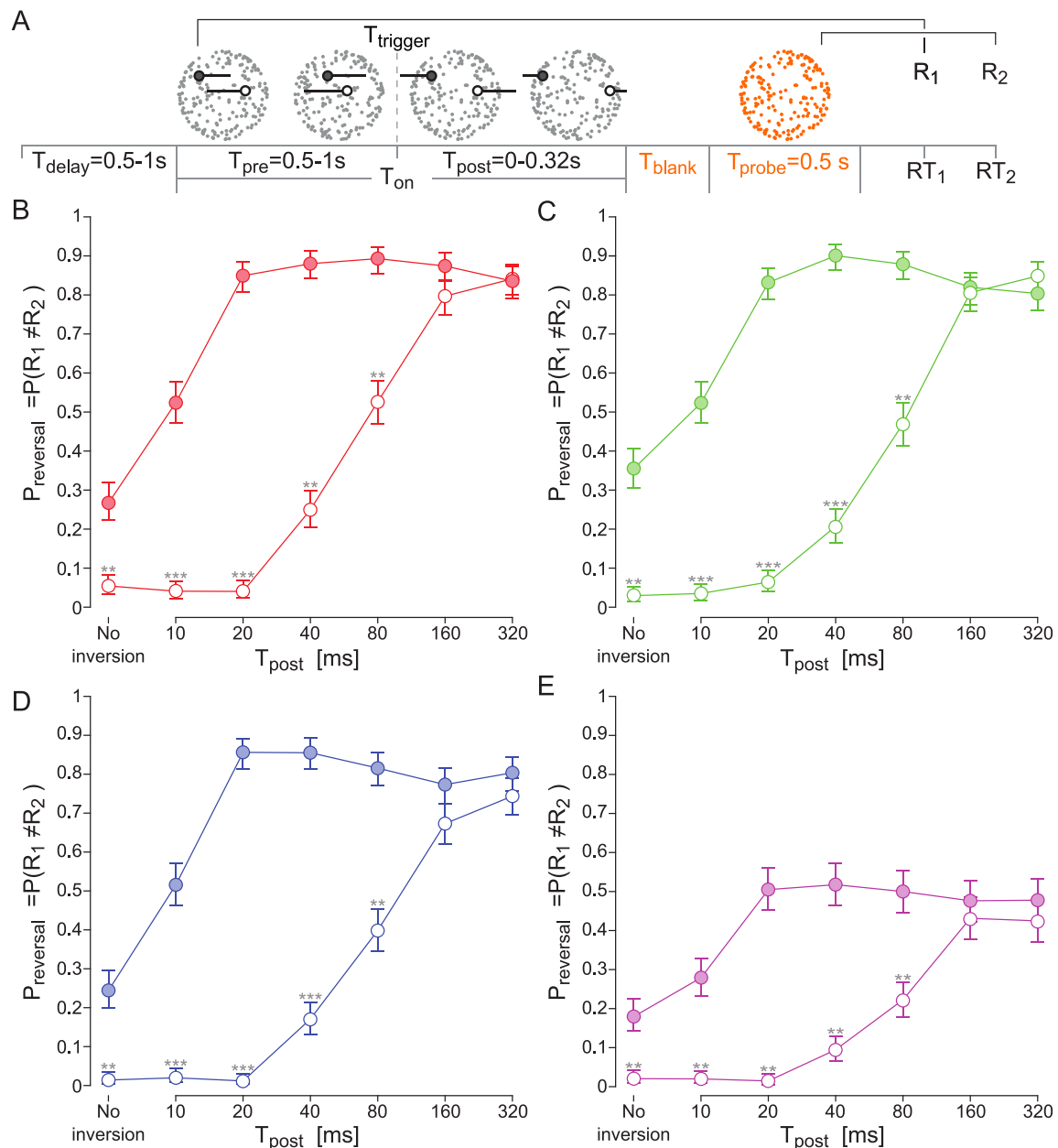


Figure 3. Experiment 2. (A) Schematic procedure. The procedure was similar to that of Experiment 1 but for a blank interval and a probe display, which followed the presentation of the main stimulus ($T_{blank} = 50$ ms, $T_{probe} = 500$ ms, both marked by orange color). The probe display was a *different* ambiguously rotating SFM sphere. Observers reported first on the initial direction of rotation of the main stimulus R_1 and then on the final direction of rotation of the probe stimulus R_2 . (B–E) Probability of a perceptual switch as the function of the postinversion interval T_{post} . Filled circles: results for Experiment 2. Open circles: results for Experiment 1 replotted for comparison. Asterisks mark statistically significant differences between the two experiments (paired-sample t test, a Bonferroni correction for multiple testing). Subfigures show data for (B) Strong (1), (C) Strong (2), (D) Medium, and (E) Weak conditions.

	Strong'	Strong	Medium	Weak
Threshold [ms]	64.2 ± 10.5	72.6 ± 10.6	75.1 ± 10.7	76.0 ± 11.0
Slope	2.61 ± 0.29	2.41 ± 0.26	2.45 ± 0.30	2.73 ± 0.53
Support [ms]	115	156.3	128.3	90.7
Guess rate	0.026 ± 0.01	0.028 ± 0.01	0.007 ± 1.92	0.014 ± 0.10
Lapse rate	0.14 ± 0.02	0.12 ± 0.03	0.25 ± 0.24	0.56 ± 0.03

Table 1. Experiment 1, summary of logistic function fits.

identical to that of Experiments 1 and 2. Both types of trials (with and without probe stimulus) were randomly mixed within a block.

Experiment 5

Nine observers (five female, four male) participated in the experiment. The procedure was similar to Experiment 2. Two conditions were used: “no inversion” and $T_{\text{post}} = 20$ ms, labeled here as “with inversion.” The blank duration was systematically varied: $T_{\text{blank}} = [50, 100, 200, 400, 800]$ ms.

Results

Experiment 1: Time necessary for the visual awareness of the perceptual reversal

In the first experiment, we sought to estimate the time interval between the trigger event and the display offset that is necessary for a perceptual reversal and/or for the visual awareness of it. To this end, we reversed the on-screen motion of all flow elements at a predefined moment of time (T_{trigger} in Figure 2A), while systematically varying the duration of a posttrigger interval. Observers reported on the initial and final directions of illusory rotation for each presentation interval.

To confirm that the observers faithfully and consistently reported their subjective perception of illusory rotation, our experimental design contained two control conditions: “no inversion” and $T_{\text{post}} = 320$ ms. The “no inversion” condition is simply a brief and unperturbed presentation of an SFM display (Figure 2B), which should lead to stable illusory rotation within the presentation interval. Conforming our expectations, the observers tended to report the same direction of rotation at the beginning and at the end of the presentation (*No inversion* in Figure 2C): P_{reversal} (S1, “no inversion”) = 0.06 [0.03–0.08] (mean and 95% confidence interval for binomial distribution), P_{reversal} (S2, “no inversion”) = 0.03 [0.01–0.05], P_{reversal} (M, “no

inversion”) = 0.01 [0.005–0.3], and P_{reversal} (W, “no inversion”) = 0.02 [0.01–0.04].

Conversely, $T_{\text{post}} = 320$ ms was the longest presentation interval, which provided observers with the best opportunity to observe and report a reversal of illusory rotation ($T_{\text{post}} = 320$ ms in Figure 2C). In agreement with prior work (Stonkute et al., 2012), a stronger motion transient due to the on-screen motion inversion produced more frequent switches of illusory rotation: P_{reversal} (S1, 320 ms) = 0.84 [0.8–0.88], P_{reversal} (S2, 320 ms) = 0.85 [0.81–0.89], P_{reversal} (M, 320 ms) = 0.74 [0.7–0.79], and P_{reversal} (W, 320 ms) = 0.42 [0.37–0.48].

The time intervals in between these two extremes represent a growing probability of reported perceptual switches (Figure 2C). Group averages across the nine observers were fitted with a logistic function. For all four conditions, the posttrigger duration that led to threshold reports of visual awareness of perceptual reversals was approximately 65 to 75 ms. Perceptual switches were reliably ($P_{\text{reversal}} \geq 0.99 \cdot P_{\text{reversal}} [320 \text{ ms}]$) reported 120 to 150 ms after the trigger event (see Table 1; Figure 2D).

Because perceptual adaptation has a strong influence on the perception of multi-stable displays (Blake et al., 1990; Kang & Blake, 2010; Pastukhov & Braun, 2011; van Ee, 2009), we analyzed its effect on induced perceptual reversals in the current study. First, we examined the effect of the short-term adaptation by comparing the probability of reversals for the shortest ($T_{\text{pre}} = 500$ ms) and the longest ($T_{\text{pre}} = 1000$ ms) pretrigger intervals but found no significant change, $t(251) = -1.6$, $p = 0.1$, paired-sample t test. Next, we repeated the same analysis but for trials from the first half versus trials from the second half of each experimental session, to assess the influence of the long-term adaptation. Here, we found a small but significant effect of adaptation, $t(251) = -3$, $p = 0.003$. However, long-term adaptation influenced only an overall probability of induced perceptual reversals (i.e., guess and lapse rate) but not the threshold or the slope of the psychometric functions (data not shown; the effect was weaker than, but qualitatively similar to, the one illustrated in Figure 4). Accordingly, we found no evidence that, for the paradigm used here, either short-term or long-term adaptation alters the speed of induced perceptual reversals (see also Experiment 2).

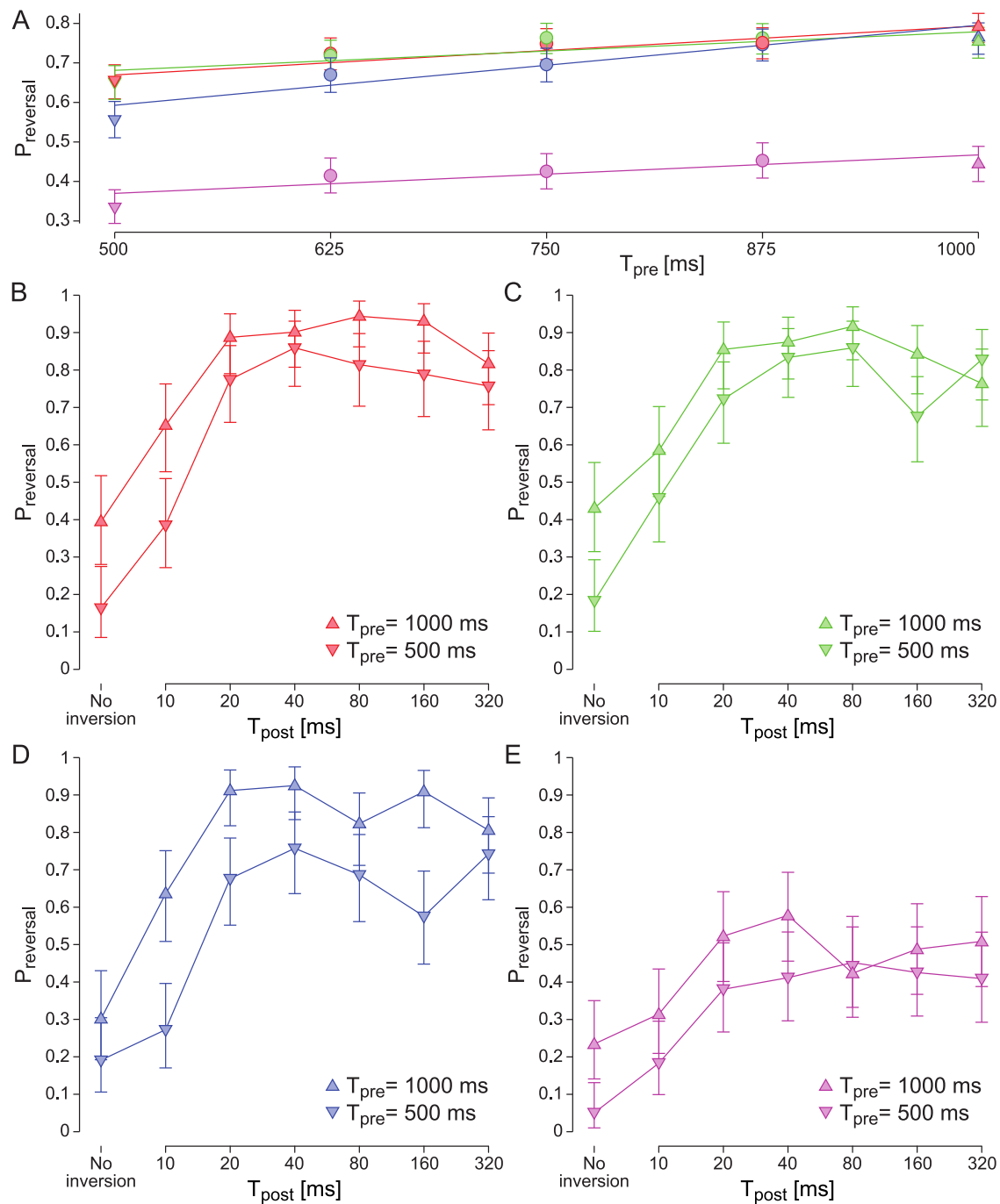


Figure 4. Experiment 2, effect of the T_{pre} interval duration. (A) Probability of the perceptual switch as a function of the posttrigger T_{post} interval duration. (B–E) Comparison between the shortest ($T_{\text{pre}} = 500$ ms, downward-pointing triangles) and longest ($T_{\text{pre}} = 1,000$ ms, upward-pointing triangles) preinversion intervals. Subfigures show data for (B) Strong (1), (C) Strong (2), (D) Medium, and (E) Weak conditions.

As an additional measure, we have analyzed the effect of both condition and posttrigger interval duration on response time and the fraction of mixed reports (see Table 2). The response times for both intervals (marked as RT_1 and RT_2 in Figure 2A) were affected by the condition and the posttrigger interval duration. However, their effect was bigger on the first response interval,

and therefore, we concentrated on RT_1 in the analysis below. With respect to mixed perception responses, we found a marginally significant effect of the posttrigger interval and a significant interaction of the effects for the second response interval, when the observers responded about the final direction of illusory rotation. The weakness of both effects is likely to be explained by a

	Factor					
	Condition (d.f. 3/24)		T_{post} (d.f. 6/48)		Condition $\times T_{\text{post}}$ (d.f. 18/144)	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
RT ₁	16.6	<0.001	11.8	<0.001	1.4	0.11
RT ₂	5.5	0.005	3.8	0.004	0.75	0.75
Unclear perception R ₁	1.7	0.2	1.2	0.3	0.9	0.57
Unclear perception R ₂	2	0.14	2.2	0.059	1.9	0.019

Table 2. Experiment 1, results for the repeated-measures analysis of variance for response time and mixed reports. *Notes:* Bold font marks statistically significant effects.

very low overall fraction of mixed reports ($1.8\% \pm 0.9\%$ of all final direction reports across all conditions and all postinterval durations). More specifically, the threshold duration was associated with longer response times (Figure 2E; RT₁["no inversion"] = 562.6 ± 87 ms, RT₁[80 ms] = 610 ± 106 ms), $t(35) = -3.5$, $p = 0.001$, paired-samples *t* test, and a higher fraction of mixed percepts (Figure 2F; mixed["no inversion"] = 0.02 [0.017–0.025] [mean and 95% confidence interval for binomial distribution], mixed[80 ms] = 0.06 [0.046–0.072]), $t(35) = -2.4$, $p = 0.023$, paired-samples *t* test. In other words, the observers were slower to respond and were less certain about the *final* direction of illusory rotation for threshold duration displays. However, a low number of mixed reports indicates that mixed phases were very brief and were rarely perceived even under the most favorable threshold conditions ($T_{\text{post}} = 80$ ms).

Next, we quantified how the motion transient's strength altered the speed of induced perceptual reversals (i.e., threshold and/or slope of a psychometric function). Comparing the two most different conditions (Strong [1] vs. Weak), we found no significant differences for the guess rate ($p = 0.98$, statistical comparison using Monte Carlo method by Palamedes toolbox) or for the slope ($p = 0.55$) parameters. However, there was a highly significant difference in the lapse rate ($p < 0.001$) and a significant difference in the threshold parameters ($p = 0.0183$; see also Figure 2D). Thus, not only did a larger pairing distance produce more frequent perceptual switches, but those switches were also perceived slightly earlier (see Table 1).

A critical aspect of the data, which would serve for an important comparison in Experiment 2, is the perception of illusory rotation for very brief posttrigger intervals ($T_{\text{post}} = [10, 20]$ ms). Not only have the observers consistently reported the same direction of rotation at the beginning and at the end of the presentation (Figure 2C), but they were also very fast to respond (Figure 2E), even faster than on trials *without* an on-screen motion

inversion: RT₁("no inversion") = 562.6 ± 87 ms (mean \pm standard deviation), RT₁(20 ms) = 536.2 ± 67 ms, $t(35) = 2.7$, $p = 0.01$ (paired-samples *t* test). In addition, they reported very few mixed percepts (Figure 2F). Thus, all three measures (subjective reports of clear perception, response times, and subjective reports on mixed perception) indicate that there was no *perceptual* difference between trials with a very brief postinterval duration ($T_{\text{post}} = [10, 20]$ ms) and trials without stimulus perturbation ("no inversion").

Experiment 2: Probing an interrupted perceptual switch

Results of Experiment 1 demonstrated that a reversal of illusory rotation was perceived only if the display presentation continued for another 80 to 150 ms after the exogenous trigger (the on-screen motion inversion). The perceptual switch itself was a very brief event, as manifested by a very low fraction of mixed percepts even for threshold conditions (see Figure 2F). The necessity for this prolonged stimulation may come from two sources. First, this time may be required for a computation of an altered on-screen motion, which in turn triggers a very brief perceptual switch. This would mean that for very brief postinversion intervals ($T_{\text{post}} = [10, 20]$ ms), the reversal of an illusory rotation was not perceived, because the sensory representation of illusory rotation remained stable at that time point, and a longer posttrigger presentation is required to trigger a reversal within them. Second, the subjective awareness of a new direction of illusory rotation may have been impeded by an earlier perception, for example via forward or backward masking (Enns & Di Lollo, 2000). In this case, a reversal of illusory rotation within sensory representations may have occurred soon after the on-screen motion inversion (e.g., already after 10- to 40-ms presentation), and the prolonged presentation would be required only to overcome masking.

To distinguish between these two possibilities, we modified Experiment 1 by appending the display sequence of Experiment 1 with a brief blank ($T_{\text{blank}} = 50$ ms) and a probe stimulus (Figure 3A, additional blank and probe intervals are marked with orange). The probe was presented for 500 ms, giving enough time for the observers to become aware of its direction of rotation, rendering forward masking irrelevant. The probe stimulus was a *different* sphere (i.e., the location of individual flow elements was different from that of the main sphere). This change interrupted the continuity of the on-screen motion as well as the continuity of 3D representations of individual dots. This way, only the representation of an interpolated 3D object could remain stable. Accordingly, we assumed that because of a very brief interruption, the illusory rotation of the

interpolated object should persist (Pastukhov & Braun, 2013) and the direction of rotation of the probe will be representative of the final direction of illusory rotation of the main (original) sphere (see Experiment 5 for a confirmation of this assumption). In all other respects, the procedure was identical to that of Experiment 1. To facilitate the comparison, trials from Experiments 1 and 2 were mixed together within a single block of an experimental session (see Methods for details).

To summarize, our experimental procedure limited the time for 2D motion extraction, interrupted persistence at the level of individual flow elements, preserved persistence at the level of an interpolated object, and gave enough time for the visual awareness of a new direction of illusory rotation to emerge.

Two postinversion interval durations were used as a control: “no inversion” and $T_{\text{post}} = 320$ ms. As in Experiment 1, the longest postinversion interval was expected to reveal the highest fraction of successfully triggered switches, and we found *no difference* between the two experiments (see $T_{\text{post}} = 320$ ms in Figure 3B through E; all p values > 0.05). This means that the final direction of illusory rotation of the probe stimulus was a reliable indicator of the final direction of illusory rotation of the main sphere (see also Experiment 5).

For the “no inversion” presentation condition, there was no on-screen motion inversion, so the perceptual switches were not exogenously triggered during the presentation of the main sphere. Therefore, as in Experiment 1, we were expecting the same perception of illusory rotation to be reported for both displays. However, we found that for all four conditions, the probability of the switch was significantly higher in Experiment 2 than in Experiment 1 (all p values below 0.01, paired-samples t test; see “no inversion” in Figure 3B through E: results of Experiment 2 are marked by filled circles, and results of Experiment 1 are marked by open circles and are replotted as a comparison): $P_{\text{reversal}}(S1, 0 \text{ ms}) = 0.27 [0.22\text{--}0.32]$ (mean and 95% confidence interval for binomial distribution), $P_{\text{reversal}}(S2, 0 \text{ ms}) = 0.36 [0.3\text{--}0.41]$, $P_{\text{reversal}}(M, 0 \text{ ms}) = 0.24 [0.2\text{--}0.3]$, and $P_{\text{reversal}}(W, 0 \text{ ms}) = 0.18 [0.14\text{--}0.23]$. This mild perceptual destabilization is typical for briefly interrupted multistable displays (Kornmeier, Ehm, Bigalke, & Bach, 2007; Orbach, Ehrlich, & Heath, 1963; Pastukhov & Braun, 2013) and is likely to reflect an accumulated perceptual adaptation/fatigue. To confirm this and analogously to the analysis we performed for Experiment 1, we assessed the effects of the short-term and long-term adaptation (respectively, the effect of the preinversion interval duration T_{pre} and the difference between trials from the first half of an experimental session vs. trials from the second half). The effect of both short-term adaptation, $t(251) = -10.1$, $p < 0.001$, paired-sample t test for $T_{\text{pre}} = 500$ ms versus $T_{\text{pre}} = 1000$ ms (see Figure 4), and long-term adaptation, $t(251) =$

-4.6 , $p < 0.001$, were highly significant. However, in both cases, adaptation shifted the entire psychometric curve vertically but not horizontally (see Figure 4). As with Experiment 1, this indicates that although accumulated adaptation significantly increases the probability of endogenously triggered perceptual reversals, it has little or no influence on their duration.

In contrast to Experiment 1, we were unable to fit group averages with a logistic function. The reason for this was that the probability of reversal reached its maximum already after $T_{\text{post}} = 20$ ms for all four experimental conditions. The probability of reversal was significantly different between the two experiments for all postinversion intervals shorter than 160 ms (paired-samples t test with a Bonferroni correction for multiple tests; statistical significance is indicated by stars in Figure 3B through E). Note that in Experiment 1, the same posttrigger intervals ($T_{\text{post}} = [10, 20]$ ms) were perceptually indistinguishable from the “no inversion” condition.

With respect to the research question we formulated for this experiment, this means that the on-screen motion extraction is complete and the reversal of perceptual dominance within sensory representations is initiated after 10 to 20 ms of the posttrigger presentation. This is particularly evident in the *Weak* condition (Figure 3E), where the fraction of reported switches reaches the maximal level for the same *Weak* condition of Experiment 1 already for the 20-ms posttrigger interval and remains at this level for all longer posttrigger intervals. In other words, our probe paradigm reveals exactly as many switches for brief posttrigger intervals of Experiment 2 as for the longest posttrigger intervals in Experiment 1. Accordingly, in Experiment 1, the lack of visual awareness of the reversal occurs despite a dominance change within the sensory representation of illusory rotation.

Because for all four conditions the maximal destabilization was reached already after the 20-ms posttrigger presentation, we were unable to assess the influence of the motion transient’s strength on the speed (or, conversely, duration) of induced perceptual reversals. This indicates that a small but significant change in the threshold between the Strong (1) and Weak conditions, observed in Experiment 1, most likely was not due to a faster perceptual reversal within a sensory representation. Instead, a stronger motion transient might have facilitated a faster propagation of this reversal into visual awareness, perhaps, by better attracting attention.

Experiment 3: Estimated time of visual awareness of the illusory rotation reversal during prolonged presentation

Although a change in the perceptual dominance within the sensory representations is initiated shortly

after the trigger event (see Experiment 2), it is possible that the visual awareness of that change consistently lags in time (Libet, 1999). In other words, the visual awareness of an exogenously triggered reversal consistently occurs not earlier than at least 40 to 60 ms after the trigger event. Therefore, we asked observer to estimate the time when they perceived the reversal and examined whether these estimates significantly and consistently lagged behind the exogenous trigger event.

To this end, we adopted a “Libet’s dot” paradigm (Libet, Gleason, Wright, & Pearl, 1983) that was previously used to estimate the time of spontaneous reversals of illusory rotation (Pastukhov et al., 2012). An ambiguously rotating sphere was accompanied by a yellow dot that was circling around the SFM display. The observers were instructed to memorize the location of the dot at the time when they perceived a reversal in the illusory rotation (see Movie 2). During the later response interval, they moved the dot to the memorized location, thus allowing us to estimate the time of the perceived reversal. The initial location of the yellow dot was randomized, and its location at any given time was not informative about the time of the trigger event.

Empirical cumulative densities functions of the estimated time of induced perceptual reversals for six observers are plotted in Figure 5 (black curves and left *y*-axis; mean estimated event times relative to the trigger event are marked by teal color). Although the observers varied in the mean estimated time of the induced perceptual reversal, they showed no systematic bias. The group average estimated time of the reversal was 1.5 ± 21 ms, and it was not significantly different from zero, $t(5) = 0.07$, $p = 0.94$. In other words, we found no tendency to perceive induced perceptual reversals as occurring significantly later than the physical trigger event. Importantly, the same six observers required at least 80 ms of continued visual presentation to develop a visual awareness of an induced switch in Experiment 1 (see red lines and right *y*-axis in Figure 5 replotted for comparison purposes). Therefore, we conclude that the results of Experiments 1 and 2 cannot be explained by a systematic delay between the time of the exogenous trigger event and the subjective perception of an illusory rotation reversal.

Experiment 4: Lack of awareness is not due to backward masking

Our results of Experiments 1 and 2 show that although the switch in perceptual dominance appears to be initiated if the presentation continues for 20 ms after the on-screen motion inversion (Experiment 2), the brief presentation times preclude the visual awareness of that switch (Experiment 1). One possible explanation for this dissociation between a sensory

change and its visual awareness is masking (Enns & Di Lollo, 2000). For example, the earlier perception of an opposite direction of motion could produce forward masking. Alternatively, it is possible that the response prompt, which appeared on the screen immediately after the main display, produced *backward* masking.

Here, we tested the latter hypothesis by replicating the “Strong (1)” condition from Experiment 1 and 2 (marked, respectively, with open and filled circles in Figure 6) but with an additional 500-ms blank interval inserted *before* the response prompt. To replicate Experiment 1, it was presented after the main SFM display (see also Figure 2A), and the stimulus onset asynchrony was increased from 20 to 320 ms to 520 to 820 ms. For the replication of Experiment 2, a blank was inserted after the presentation of the *probe* display (see also Figure 3A).

The results of Experiment 4 are presented in Figure 6. If a delay of visual awareness of the perceptual reversal in Experiment 1 was due to backward masking, the additional blank should have attenuated its effect. Therefore, the number of reported perceptual reversals for brief T_{post} durations for the replication of Experiment 1 should have increased, and the filled-circles curve in Figure 6 should have become similar to the open-circles curve (curves correspond, respectively, to replications of Experiments 1 and 2). However, the curves in Figure 6 both qualitatively and quantitatively match the results of Experiments 1 and 2. Specifically, in replication of Experiment 1, short postinversion intervals ($T_{\text{post}} < 40$ ms) lead to consistent reports of perceptual stability. We conclude that the lack of awareness is not explained by backward masking from the response prompt.

Experiment 5: The direction of illusory rotation in the probe display reflects the most recent perceptual state before the interruption

The experimental procedure for the Experiment 2 was based on the assumption that the direction of illusory rotation of the probe displays reflects the most recent (final) state of the main display before the interruption. This assumption was based on earlier work that showed that for brief blank intervals, the perceptual dominance is stabilized by neural persistence—a quickly decaying activity of an originally dominant neural population (Pastukhov & Braun, 2013). However, it is possible that the perceptual dominance of the probe display reflected another history effect, such as a sensory memory of multistable displays (Adams, 1954; Leopold, Wilke, Maier, & Logothetis, 2002; Orbach et al., 1963; Ramachandran & Anstis, 1983).

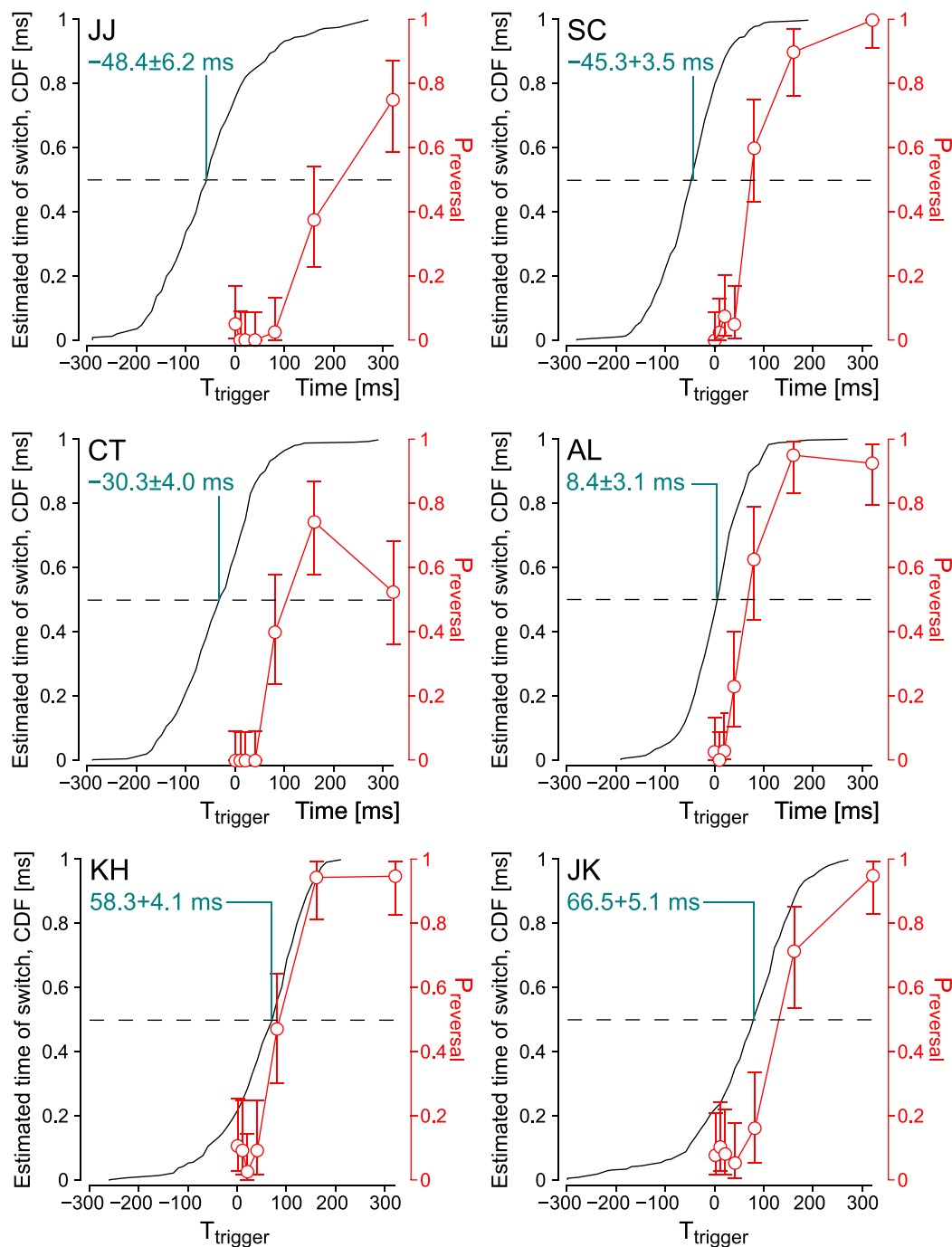


Figure 5. Estimated time of an illusory rotation reversal, individual observers. *Black color and left vertical axis.* Empirical cumulative densities function of an estimated time when a perceptual reversal occurred, relative to the time of the trigger event (T_{trigger}). CDF = 0.5 corresponds to the mean estimated time of a perceptual switch (marked by teal color). Although the accuracy and the bias of an estimated switch time vary between individual observers, we found no systematic tendency to perceive an exogenously triggered switch to occur significantly later than the trigger event. Red color and right vertical axis. Results of the Strong (1) condition of Experiment 1 replotted for comparison. In contrast to Experiment 3, all six observers were very similar in that they required >80 ms of continued visual presentation to become aware of an induced perceptual reversal.

To control for this possibility, we replicated Experiment 2 using only two conditions: “no inversion” and $T_{\text{post}} = 20$ ms (labeled here as “with inversion”) but with a broad range of the blank interval durations

($T_{\text{blank}} = [50, 100, 200, 400, 800]$ ms). The purpose of the latter was to dissociate the influence of two history effects in question. Whereas neural persistence decays within 400 to 500 ms (Pastukhov & Braun, 2013),

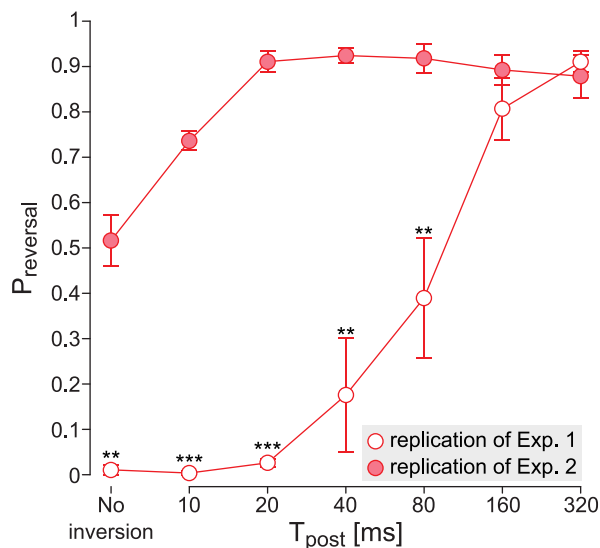


Figure 6. Experiment 4. An additional blank before the response interval minimizes the masking but has no effect on perceptual reversals. Probability of a perceptual switch is plotted as a function of the postinversion interval T_{post} . Filled circles: replication of Experiment 2. Open circles: replication of Experiment 1. Asterisks mark the statistically significant differences between the two conditions (paired-sample t test, the Bonferroni correction for multiple testing).

sensory memory is characterized by very long decay times of dozens of seconds or even minutes (Leopold et al., 2002). Accordingly, if the perceptual dominance of the probe displays was determined by sensory memory, the blank interval duration should have a minimal effect. Conversely, if illusory rotation was stabilized by neural persistence, this effect should be absent for blank intervals longer than 400 to 500 ms.

The results of Experiment 5 are plotted in Figure 7. The “no inversion” condition (gray filled circles in Figure 7) served as a baseline to determine the effect of the blank interval duration on the probability of perceptual reversals in the absence of exogenously triggered perceptual switches. The results revealed an inverted U-shape and were qualitatively consistent with previous reports (Kornmeier et al., 2007; Orbach, Ehrlich, & Vainstein, 1963; Pastukhov & Braun, 2013). For the “with inversion” condition (orange open circles in Figure 7), the $T_{\text{blank}} = 50$ ms duration was identical to that of Experiment 2 and replicated a reliable switching effect of the prior on-screen motion inversion. Critically, this effect disappeared for blanks longer than 100 ms. This short-lived effect is consistent with neural persistence/hysteresis but not with sensory memory of multistable displays or any other bias that operates at the time scale of seconds. We conclude that the perceptual dominance of the probe displays reflects the latest perceptual state of a prior display.

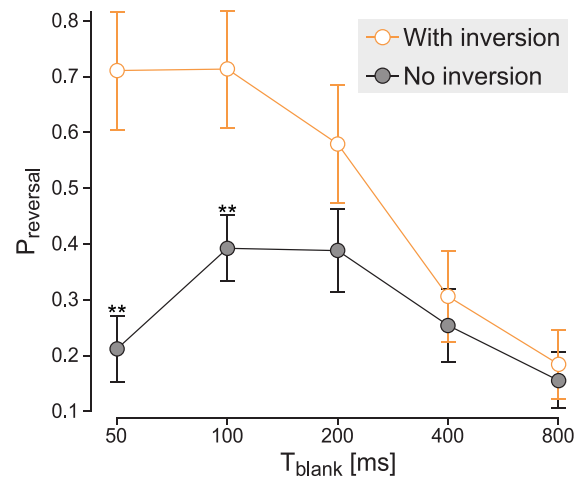


Figure 7. Experiment 5. Probability of the perceptual switch as a function of the blank interval for trials with (open gray circles) and without (filled orange circles) an on-screen motion inversion. The influence of the on-screen motion inversion was significant only for very short blank intervals ($T_{\text{blank}} < 200$ ms). Asterisks mark statistically significant differences between “with inversion” and “no inversion” conditions (paired-samples t test, the Bonferroni correction for multiple testing).

Discussion

Here, we investigated the perception of an exogenously triggered reversal of illusory rotation in SFM displays. We report that the reversals themselves are very brief (Experiment 1) and that the change in dominance in the sensory representation is initiated shortly after the trigger event, as even a 20-ms posttrigger presentation duration is sufficient for this (Experiment 2). However, the observers become aware of that switch only if the presentation continues for at least 80 ms after the trigger event (Experiment 1). This effect cannot be explained either by a systematic delay of visual awareness (Experiment 3) or by backward masking (Experiment 4). Therefore, we conclude that exogenously triggered reversals are brief and can occur in the absence of visual awareness.

Induced perceptual switches occur in the absence of visual awareness

The results of Experiments 1 and 2 demonstrate that although a reversal of the perceptual dominance within the sensory representations of illusory rotation is initiated within 20 ms after the trigger event, the observers become aware of that only if the presentation continues for at least 80 ms. If the presentation is curtailed using shorter posttrigger intervals ($T_{\text{post}} = 10$ –20 ms), the observers fail to notice the reversal, and

both their responses and, presumably, perception are *qualitatively and quantitatively* similar to that of an unperturbed stable illusory rotation (see Experiment 1). Earlier work showed that exogenously triggered reversals also occur in the (near) absence of attention (Stonkute et al., 2012). Therefore, we can conclude that neither awareness nor attention is necessary for *exogenously* triggered reversals of perceptual dominance in SFM.

Our results raise further questions about the contribution of top-down factors such as attention and visual awareness to perceptual switches. Although shifts of attention were postulated as a possible mechanism behind perceptual reversals (Leopold & Logothetis, 1999) and their causal effect on multistable perception is well documented (Brouwer & van Ee, 2006; Chong, Tadin, & Blake, 2005; Mitchell, Stoner, & Reynolds, 2004), later work demonstrated that attention may not be required for *spontaneous* reversals (Pastukhov & Braun, 2007; Roeber, Vesper, Schröger, & O’Shea, 2011; but see Brascamp & Blake, 2012; Zhang, Jamison, Engel, He, & He, 2011). Similarly, not only exogenously triggered but also endogenously triggered (spontaneous) reversals can occur without visual awareness (Brascamp, Blake, & Knapen, 2015; Platonov & Goossens, 2014).

The similarity between our results and the findings on *endogenously triggered* reversals indicates that neural populations responsible for initiation of spontaneous perceptual switches are likely to be located in sensory regions of the brain. This idea fits well with prior psychophysical experiments (Alais, Cass, O’Shea, & Blake, 2010; Brascamp, van Ee, Noest, Jacobs, & van den Berg, 2006; van Ee, 2009), modeling (Noest, van Ee, Nijs, & van Wezel, 2007; Shpiro, Moreno-Bote, Rubin, & Rinzel, 2009), and recent imaging studies (Brascamp et al., 2015; Frässle et al., 2014; Knapen et al., 2011). Accordingly, it strengthens the idea that although both awareness and attention modulate multistable perception and the occurrence of perceptual reversals, they are not causally responsible for them.

Exogenously versus endogenously triggered perceptual reversals

The presented study used *exogenously triggered* perceptual reversals, and this warrants a question about how much our findings can tell us about general mechanisms behind multistable perception and *spontaneous* perceptual switches. However, one must remember that a spontaneous reversal can be triggered by internal forces as divergent as an involuntary eye movement, an intrinsic neural noise, or a shift of attention. Accordingly, even if a conceptual difference between exogenously and endogenously triggered

perceptual reversals is clear, it is less obvious how individual endogenous triggers differ from exogenous ones in terms of events occurring at the level of neural representations.

For example, although a multistable display itself may remain constant throughout the entire presentation, its retinal image never does. Even when the observers are faithfully fixating, the retinal image of a display is constantly changing because of eye tremor, drift, and microsaccades (Martinez-Conde, Macknik, & Hubel, 2004). These changes of the retinal image are endogenously generated but can trigger a perceptual reversal (van Dam & van Ee, 2006), just like exogenous changes due to an inversion of the on-screen motion or due to a brief change of an image contrast (Kim, Grabowecy, & Suzuki, 2006).

Furthermore, all neural representations, starting already at the retinal level, are intrinsically noisy (Faisal, Selen, & Wolpert, 2008). This means that all neural representations involved in multistable perception, both ones that can be considered “inputs” in modeling terms and those that correspond to competing percepts, undergo constant random changes. These noise-driven fluctuations in neural representations are currently thought to be the main source of spontaneous reversals based on both experimental (Brascamp et al., 2006; Pastukhov & Braun, 2011; van Ee, 2009) and modeling (Moreno-Bote, Rinzel, & Rubin, 2007; Noest et al., 2007; Pastukhov et al., 2013) perspectives. Just as an inversion of the on-screen motion, these noise-induced fluctuations are transient and do not produce a long-lasting bias in favor of a particular perception. And, similar to the on-screen motion inversions, they may trigger a reversal in the perceptual dominance when they occur at an appropriate moment (Moreno-Bote et al., 2007; Noest et al., 2007). However, just like exogenous triggers, they may also be ignored by the visual system, manifesting themselves as brief periods of destabilization (Brascamp et al., 2006; Naber, Frässle, & Einhäuser, 2011; Pastukhov & Braun, 2011).

Taken together, this suggests that the difference between the endogenous noise-driven transient changes in neural representations and the exogenous-driven transient changes in neural representations may be of a quantitative rather than qualitative nature. Accordingly, the interpretation of our results and of other work on the exogenously triggered reversals will be facilitated primarily by a better understanding of divergent endogenous causes of spontaneous reversals.

Duration of perceptual switches

Experiment 1 demonstrated that, in agreement with current models of multistable perception (Laing & Chow, 2002; Moreno-Bote et al., 2007; Moreno-Bote,

Knill, & Pouget, 2011; Noest et al., 2007), the duration of perceptual switches in SFM is extremely brief: The observers rarely reported unclear perception even under the most favorable threshold conditions (80 ms in Experiment 1). These nearly instantaneous switches may appear to be drastically faster than longer and easily noticeable transitions between two clear percepts in binocular rivalry (Blake, O’Shea, & Mueller, 1992; Brascamp et al., 2006; Pastukhov & Braun, 2011). However, it is possible that the difference lies not in the nature of two multistable displays but in the exact definitions of perceptual switches and perceptual transitions.

For binocular rivalry, a perceptual transition can be defined as a perception that is different from the state of exclusive visibility and typically includes piecemeal rivalry as well as episodes of binocular fusion. Although both of these perceptual states clearly differ from exclusive visibility, they also do not correspond to the perceptual switch. Binocular fusion is a default and different state of binocular vision (Wolfe, 1983). The piecemeal rivalry is the patchy appearance when some spatial regions are dominated by one eye whereas other regions are dominated by the other eye. It is more likely to occur for bigger visual displays (Blake et al., 1992; Kang, 2009; O’Shea, Sims, & Govan, 1997) and is reduced in the presence of additional grouping factors such as rotation (Haynes, Deichmann, & Rees, 2005). Accordingly, although one can talk about “mixed perception” with respect to the entire image, individual patches are in exclusive visibility states. Accordingly, although periods of nonexclusive visibility may be long, they do not necessarily correspond to transient reversals of perceptual dominance postulated in current models of multistable perception (Laing & Chow, 2002; Moreno-Bote et al., 2011, 2007; Noest et al., 2007).

To summarize, perceptual reversals in SFM are extremely brief, and it is for future research to determine whether the same is true for perceptual switches in binocular rivalry and other multistable displays. However, it will be important to distinguish between perceptual *switches* and alternative perceptual *states*, such as piecemeal rivalry and binocular fusion.

Conclusions

We report that induced perceptual reversals of illusory rotation in SFM displays are very brief and occur in the absence of visual awareness.

Keywords: structure-from-motion, perceptual alternations, multistable perception, kinetic-depth effect, perceptual reversals, visual awareness

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