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Transformation priming helps to disambiguate sudden changes of sensory inputs

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ABSTRACT

Retinal input is riddled with abrupt transients due to self-motion, changes in illumination, object-motion, etc. Our visual system must correctly interpret each of these changes to keep visual perception consistent and sensitive. This poses an enormous challenge, as many transients are highly ambiguous in that they are consistent with many alternative physical transformations. Here we investigated inter-trial effects in three situations with sudden and ambiguous transients, each presenting two alternative appearances (rotation-reversing structure-from-motion, polarity-reversing shape-from-shading, and streaming-bouncing object collisions). In every situation, we observed priming of transformations as the outcome perceived in earlier trials tended to repeat in subsequent trials and this repetition was contingent on perceptual experience. The observed priming was specific to transformations and did not originate in priming of perceptual states preceding a transient. Moreover, transformation priming was independent of attention and specific to low level stimulus attributes. In summary, we show how "transformation priors" and experience-driven updating of such priors helps to disambiguate sudden changes of sensory inputs. We discuss how dynamic transformation priors can be instantiated as "transition energies" in an "energy landscape" model of the visual perception.

1. Introduction

Our brain must reconstruct the outside visual world from a sensory evidence that is always incomplete and is always intrinsically ambiguous (Gregory, 2009; Metzger, 2009; Yuille & Kersten, 2006). To make things worse retinal input constantly changes due to self-motion, changes in illumination, object-motion, etc. This poses an enormous challenge, as very different physical changes can produce identical changes in sensory evidence. An object changing its size (an inflated frog) and an object getting closer (you are walking toward the frog) could produce the same change in sensory evidence (a change in the size of a retinal image) (Combe & Wexler, 2010; Koenderink, 1986). A change of a retinal projection's shape may imply that object moved (a leaf was moved by a wind), that you moved (you walked past the tree), or some combination of both (a leaf was moved by a wind as you were walking past the tree) (Wexler, Panerai, Lamouret, & Droulez, 2001). An activation-pattern of cone cells on the retina that corresponds to somebody's face may change because the person blushed (surface has changed) or because the person stepped from a direct sunlight into an ambient illumination in the shadow or because a cloud obstructed the sun (illumination has changed) (Jameson & Hurvich, 1989). Ambiguity of change in sensory evidence makes it hard for the perceptual system to identify a unique physical cause and to determine whether constancy of a particular visual feature must be maintained. Yet, this unique physical cause is all that matters and is what our visual system is trying to correctly represent in perception.

None of the examples above correspond to a rare and exceptional event. On the contrary, they are the norm for the dynamic environment that we actively explore and which is full of objects, animals, clouds, wind, etc. It is the ubiquity of these events that raises the question of how the visual system resolves their dynamic ambiguity. The general answer to the problem is to gather and exploit prior knowledge (Friston, Breakspear, & Deco, 2012; Gregory, 2009; Metzger, 2009; Yuille & Kersten, 2006), and this process has been well studied from both behavioral (Kristjánsson

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& Campana, 2010; Pastukhov & Braun, 2011, 2013b) and theoretical (Friston et al., 2012; Pastukhov, García-Rodríguez, et al., 2013) perspectives, even though the neural implementations are still poorly understood (Daw, O'Doherty, Dayan, Seymour, & Dolan, 2006). The main focus of prior research was the knowledge about physical states (Hansen, Olkkonen, Walter, & Gegenfurtner, 2006; Weiss, Simoncelli, & Adelson, 2002; Yang & Purves, 2003; Yuille & Kersten, 2006), however this type of knowledge serves only as a weak constraint because the number of transformations by far outstrips the number of states.

Accordingly, our visual system also relies on the knowledge about physical transformations (in addition to, and independent of, the similar information on physical states) to determine the most likely cause of a change in sensory evidence. Because of that in examples above certain transformations are more likely to be perceived than other. Previous work of on transformation priors (Barbur & Spang, 2008; Combe & Wexler, 2010; Pastukhov, Vonau, & Braun, 2012; Tse, 2006; Tse & Logothetis, 2002; Wexler & van Boxtel, 2005) demonstrated their importance to the dynamic perception and their link to ecological constraints of the outside world. Present work extends this by asking the question whether this prior knowledge is gathered from the recent perceptual experience or can be considered to be static.

2. Materials and methods

2.1. Observers

All participants had normal or corrected-to-normal vision. Observers were naive to the purpose of the experiments and were paid for their participation. Procedures were approved by the medical ethics board of the Otto-von-Guericke Universität, Magdeburg "Ethik-Komission der Otto-von-Guericke-Universität an der Medizinischen Fakultät" and were in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

2.2. Apparatus

Stimuli were generated with MATLAB using the Psychophysics Toolbox (Brainard, 1997). Stimuli were displayed on a CRT screen (Iiyama VisionMaster Pro 514, iiyama.com) with a spatial resolution of 1600×1200 pixels and refresh rate of 100 Hz. The viewing distance was 73 cm, so that each pixel subtended approximately 0.019°. In all experiments, background luminance was kept at 36 cd/m^2. The experimental room was lit dimly (ambient luminance at 80 cd/m^2).

2.3. Stimuli and procedure

2.3.1. Experiment 1a. Structure-from-motion

Eighteen observers participated in the experiment. Structure-from-motion (SFM) stimulus (see Fig. 1A and Movies 2–3) consisted of 100 dots distributed randomly over the surface of the illusory sphere. The diameter of the sphere was 5°, rotation period 0.2 Hz. The diameter of a single dot was 0.057°, luminance – 110 cd/m^2. The dots were semi-transparent, i.e. the luminance of the overlap was a sum of individual luminance levels. This provided no cue on which dot is "on top" during the overlap to exclude any possible occlusion effects. Individual trials consisted of a random stimulus onset delay (0.5–1 s, drawn from a uniform distribution), presentation interval (1.5 s) and response interval (unspeeded response, mean duration 587.9 + 19.4 ms), see Movies 2–3. Planar motion of all dots was inversed at a random time-point T_{change} between 0.5 s and 1 s after the stimulus onset (drawn from a uniform distribution), see Fig. 1D and Movies 2–3. Observers used arrow keys to report on the initial and the final direction of illusory rotation. Observers reported unclear/mixed percept by pressing the "down" arrow key (2.31 ± 0.63% of total trials). Each block contained 40 On- and Off-intervals (400 trials per observer).

2.3.2. Experiment 1b. Shape-from-shading

Nine observers participated in the experiment. Shape-from-shading (SFS) stimulus (Fig. 1B and Movie 4) had outer diameter of 2° and inner diameter of 0.7°, gradient rings had width of 0.3°. Stimulus orientation was defined in the direction of gradient. The display in Fig. 1B corresponds to the orientation of 90°. Individual trials consisted of a random stimulus onset delay (0.5–1 s, drawn from a uniform distribution), presentation interval (1.5 s) and response interval (unspeeded response, mean duration 969.9 ± 164.6 ms). The initial orientation of the display was pseudo-randomly selected from a uniform distribution with a 22.5° step. The display was rotated by 180° at a random time-point T_{change} between 0.5 s and 1 s after the stimulus onset (drawn from a uniform distribution), see Fig. 1E and Movie 4. Observers reported on the initial and final state of the perceived shape using arrow keys (*up* – concave, *down* – convex). Observers reported unclear/mixed percept using a "left" arrow key (3.39 ± 1.34% of total trials). A single experimental session consisted of twelve blocks. Each block contained 64 On- and Off-intervals (768 trials per observer, 64 trials per orientation).

2.3.3. Experiment 1c. Streaming-bouncing

Nine observers participated in the experiment. Streaming-bouncing (SB) stimulus (Fig. 1C and Movie 5) consisted of two symmetric trapezoid objects with identical height and bottom sides (both 2°) but different upper sides (0.8° and 1.2°). Objects moved with a speed of 7°/s along linear trajectories, so that they crossed behind a circular occluder (Ø3°, total presentation duration 1.5 s), see Fig. 1F and Movie 5. Response was unspeeded, mean duration 351.9 ± 62.7 ms. In half of the trials (selected randomly), objects continued the linear motion, whereas in the other half of the trials they "bounced" off each other. Observers used arrow keys to report whether they perceived streaming (objects continued the linear motion, *left arrow*) or bouncing (objects "bounced" off each other, altering their motion path, *right arrow*). A single experimental session consisted of ten blocks. Each block contained 80 On- and Off-intervals (800 trials per observer).

2.3.4. Experiment 2

Nine observers participated in the experiment. Procedure was identical to that of Experiment 1a. Display in the baseline condition was identical to that in Experiment 1a. In the second condition, the planar motion inversion was omitted on half of randomly selected trials, producing a nearly unambiguous perception of stable illusory rotation.

2.3.5. Experiment 3a. Specificity to location

Six observers participated in the experiment. Structure-from-motion (SFM) stimulus was identical to that used in the main experiment. Procedure was identical to that of Experiment 1a except for the location of the display. It was presented 2.5° to the left or to the right off the fixation. Location was altered on every trial, initial location at the beginning of the block was randomized.

2.3.6. Experiment 3b. Specificity to axis of rotation

Six observers participated in the experiment. Structure-from-motion (SFM) stimulus was identical to that used in the main experiment. Procedure was identical to that of Experiment 1a except for the axis of rotation of the display. It was presented as rotating either around a vertical or around a horizontal axis. The

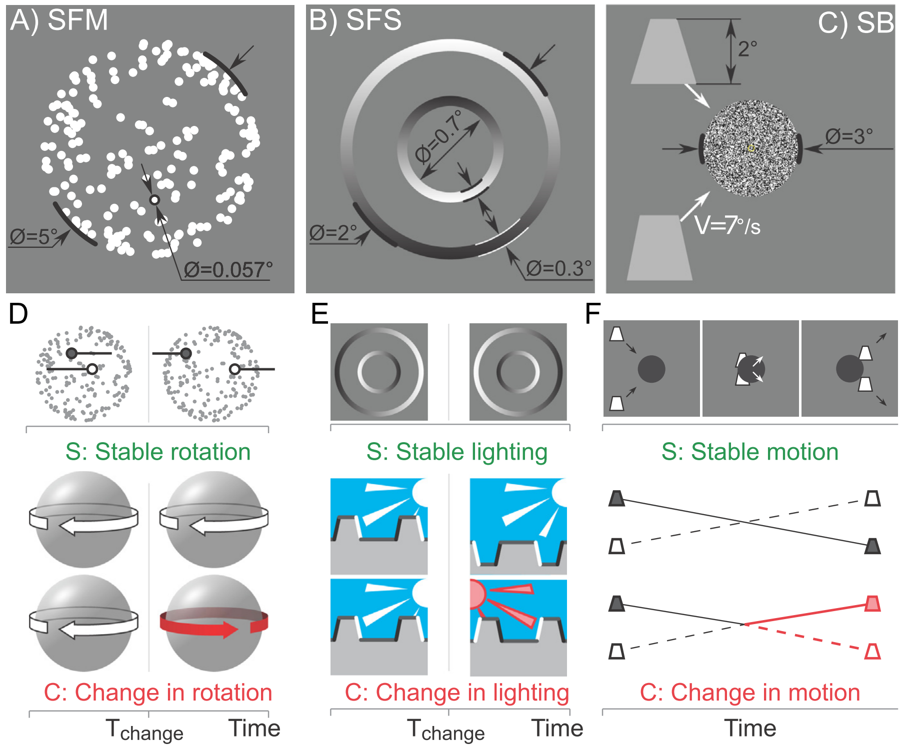

Fig. 1. Experiment 1, schematic displays (A–C) and procedure (D–F). (A and D) Structure-from-motion. (B and E) Shape-from-shading. (C and F) Streaming-bouncing display. (D–F) For each visual sequence two alternative perceptual transformations are marked as S (a selected visual feature remains stable) and C (a selected visual feature has changed). (D) Sudden change in a planar flow of a structure-from-motion display (top row, an inversion of a planar motion is indicated for two example dots), can be perceived either as stable illusory rotation (middle row) or as a change in illusory rotation (bottom row). See also Movies 2–3. (E) A change in stimulus orientation of a shape-from-shading display (top row), can trigger an inversion of the shape, so that light remains stable (middle row) or as change in light location with the shape remaining constant (bottom row). See also Movie 4. (F) When motion paths of two objects cross behind an occluder (top row), it produces either a perception of stable motion ("streaming", middle row) or of a change in linear motion due to an elastic impact ("bouncing", bottom row). See also Movie 5.

axis of rotation was altered on every trial, the initial axis of rotation at the beginning of the block was randomized.

2.3.7. Experiment 3c. Specificity to object's shape

Eight observers participated in the experiment. The sphere structure-from-motion (SFM) stimulus was identical to that used in the main experiment. The band object consisted of 250 dots distributed randomly over the surface of the illusory band, see Movie 6. Object dimensions and speed of rotation, as well as that of dots were identical to the sphere stimulus. Procedure was identical to that of Experiment 1a except for two objects' shapes. The shape of the SFM object was altered on every trial.

3. Results

3.1. Experiment 1. Perception of ambiguous transient changes of sensory evidence

In our first experiment we sought to establish how internal variables (prior knowledge) determine the perception of ambiguous transient changes in sensory inputs on consecutive trials.

When studying influence of internal variables (prior knowledge) on *perceptual states*, one often relies on multi-stable displays (Blake & Logothetis, 2002; Leopold & Logothetis, 1999). The latter are visual stimuli that are compatible with several distinct perceptual interpretations. Therefore, while sensory inputs remain constant, changes of internal variables produce different and alternating perception (see Movie 1 for an example of a multi-stable structure-from-motion display). In turn, observer's reports on her/his perception, allow experimenter to infer corresponding changes to these hidden internal variables. This approach is particularly fruitful when studying changes of internal variables over time (Leopold, Wilke, Maier, & Logothetis, 2002; Nawrot & Blake, 1991; Pastukhov & Braun, 2008, 2013a, 2013b; Pastukhov, Lissner, Füllekrug, & Braun, 2014).

Here, we employed a similar experimental paradigm, but instead of presenting constant ambiguous sensory evidence (as in multi-stable displays), we presented display sequences that had an ambiguous transient *change* of sensory evidence. In all three displays described below, the same sudden and ambiguous change in sensory inputs can lead to two distinct perceptual outcomes: stability (constancy) or a change of a particular visual feature. Hence, as with perceptual states, observer's perception on a given trial is dictated by a current state of internal variables (prior knowledge). By analogy to multi-stable displays, the procedure employed here can be described as intermittently presented ambiguous changes of sensory inputs.

The three dynamic visual displays we used in Experiment 1 are schematically illustrated in Fig. 1. For the structure-from-motion display (SFM, see Fig. 1A, D and Movies 2–3), a change in a planar flow may be perceived either as a stable illusory rotation, which is accompanied by a slight positional displacement of individual flow elements, or as a change in the direction of illusory rotation (Pastukhov et al., 2012). For the shape-from-shading display (SFS, see Fig. 1B, E and Movie 4), a sudden 180° rotation could be interpreted either as an inversion of the shape's depth while the location of the light source remains stable, or as a change in the location of a light while the shape remains constant. Finally, in the streaming-bouncing paradigm (SB, see Fig. 1C, F and Movie 5), two objects may be seen as moving along linear paths ("streaming" through each other), or as suddenly changing their motion ("bouncing" off each other) as they pass behind the occluder (Kawabe & Miura, 2006). For all three cases, the change to the visual display remains constant and perceived outcome is determined primarily by internal variables (prior knowledge).

To quantify whether or not perceptual outcomes of the same ambiguous sensory change on consecutive trials are independent, we compared two conditional probabilities $P(\mathrm{S}[i]|\mathrm{S}[i-1])$ and $P(\mathrm{S}[i]|\mathrm{C}[i-1])$. $P(\mathrm{S}[i]|\mathrm{S}[i-1])$ is the conditional probability of seeing stability on the current trial (S[i]) given that stability was reported as an outcome of the preceding trial (S[$i-1$]). This conditional probability is depicted by green/dark bars in Fig. 2. $\mathrm{P}(\mathrm{S}[i]|\mathrm{C}[i-1])$ is the conditional probability of seeing a stability on the current trial (S[i]) given that change was reported as an outcome of the preceding trial (C[$i-1$]). This is marked by red/light bars in Fig. 2. Lack of a significant difference between the two conditional probabilities that represent opposite history of perceptual stability implies that observers' perception on two consecutive trials was independent. Conversely, a significant difference between the two (e.g. green/dark bars are consistently higher than the red/light ones or vice versa) indicates that perception on consecutive trials was correlated. The sequential dependence can when be defined as $\Delta P(1) = P(\mathrm{S}[i]|\mathrm{S}[i-1]) - P(\mathrm{S}[i]|\mathrm{C}[i-1])$.

Results for all observers and displays are depicted in Fig. 2 and demonstrate that perception of ambiguous changes in sensory inputs on consecutive trials was not independent. A paired-sample t-test showed significant difference between two conditional probabilities for all three displays: for SFM, $t(17) = 4.9$, $p < 0.001$; for SFS, $t(8) = 7.5$, $p < 0.001$; for SB, $t(8) = 5.8$, $p = 0.0003$. Specifically, perceptual stability tended to be followed by stability and, conversely, perception of change also tended to repeat itself on a consecutive trial. Conditional probabilities were significantly different for lags of up to 6 trials for SFM, 7 trials for SFS, and 3 trials for SB ($p < 0.05$ for a paired-sample t-test without the correction for multiple comparisons). Over the course of an experimental session difference between conditional probabilities is reflected in "slow drifts" of probability of stable perception (see Fig. 3).

3.2. Experiment 2: Changes to internal variables reflect recent experience

Experiment 1 demonstrated that internal variable that influences perception of ambiguous changes of sensory evidence varies gradually over time (see Fig. 3). These temporal fluctuations could reflect an earlier perceptual experience but can also be explained by internal phasic factors. Accordingly, we investigated whether these variations of internal variables over time reflect observers' perceptual experience or are independent of it. To address this issue, we examined whether perception of ambiguous change in planar motion for SFM displays was modified when observers were exposed to a large number of episodes with stable illusory rotation and without an ambiguous sensory change.

First, we repeated Experiment 1 to establish the baseline probability of stable illusory rotation over the entire experimental session ($P_{\mathrm{baseline}}(\mathrm{C}[i]) = 0.32 \pm 0.07$, dark bars in Fig. 4, SFM display only). We also observed the same sequential dependence as in Experiment 1 ($\Delta P[1] = 0.22 \pm 0.09$, $t(8) = 2.7$, $p = 0.026$).

Next, we modified the experiment so that on half of randomly selected trials the planar motion remained unperturbed. In the absence of the planar motion inversion, illusory rotation on these trials was almost always perceived as stable ($P_{\mathrm{unperturbed}}(\mathrm{C}[i]) = 0.97 \pm 0.01$) and, hence, was nearly unambiguous with respect to perception of transformations. To resolve the question of whether the drift of perceptual stability over time depends on observers' perceptual experience, we analyzed probability of stability during remaining trials that contained the inversion of planar motion. Note that if changes to internal variables are independent of perceptual experience, we would expect the overall probability of stability to remain the same. Instead, we found that observers were significantly more likely to report stability (light bars in Fig. 4, $P_{\mathrm{test}}(\mathrm{C}_i) = 0.44 \pm 0.08$, $t(8) = 7.8$, $p < 0.001$, paired samples t-test for P_{baseline} vs. P_{test}).

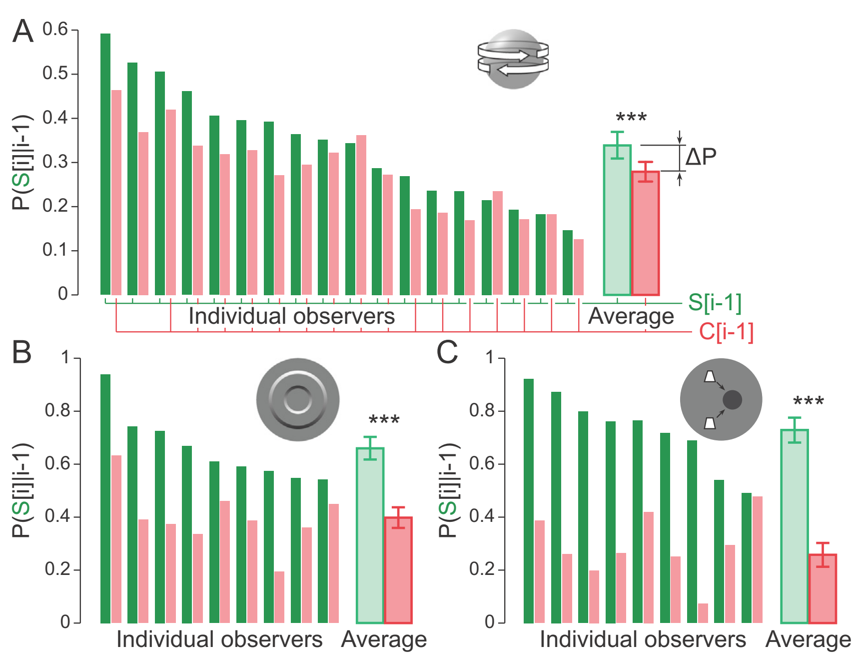

Fig. 2. Experiment 1, results. Same perceptual outcome is more likely to be perceived again on the following trial compared to an alternative. Bars depict conditional probabilities of stable perception given the outcome of the previous trial. Green/dark bars depict $P(\mathrm{S}[i]|\mathrm{S}[i-1])$, red/light bars depict $P(\mathrm{S}[i]|\mathrm{C}[i-1])$. Error bars correspond to 95% for binomial distribution, asterisks indicate statistical significance for group averages (see text for detials). (A) Structure-from-motion. (B) Shape-from-shading. (C) Streaming-bouncing. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

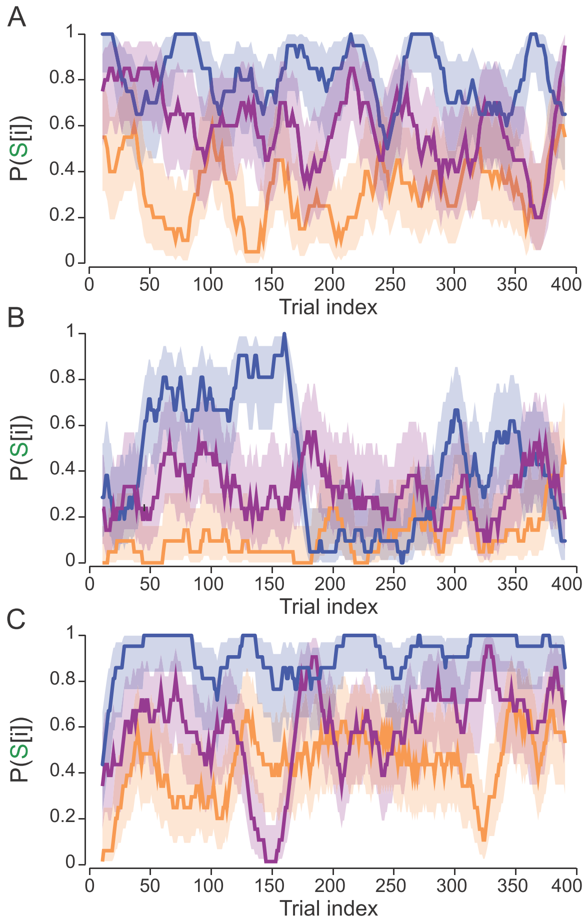

Fig. 3. Probability of perceptual stability as a function of time. Mean probability (solid lines) and 95% confidence interval for binomial distribution (stripes) for three example observers. The sliding window was 20 trials wide and moved with a step of 1 trial. (A) Structure-from-motion. (B) Shape-from-shading. (C) Streaming-bouncing display.

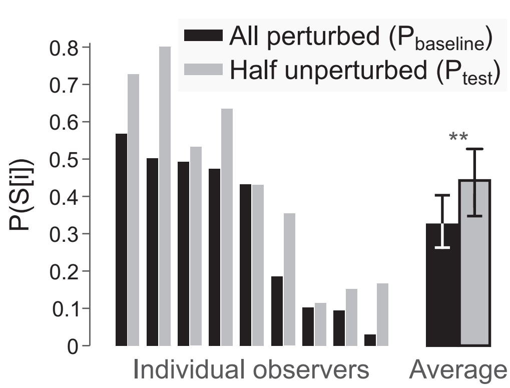

Fig. 4. Experiment 2, perception of the ambiguous inversion of planar motion was biased towards stability when observers were exposed to a large number of episodes with stable illusory rotation and without an ambiguous sensory change. Dark bars, $P_{baseline}$: probability of stable perception when all trials contained a planar motion inversion. Light bars, P_{test}: probability of stable perception on trials with planar motion inversion, when on half of the randomly selected trials the planar motion remain unperturbed. See text for details.

This demonstrates that the perception on trials with an ambiguous change of sensory inputs is biased by the recent experience of stable perception in unperturbed trials. In other words, a recent perceptual experience *primes* perception of transformations on the following trial. Also, this experiment demonstrated that the induction of *transformation priming* does not require the physical change in the display and that the perceptual experience is sufficient.

3.3. Transformation priming cannot be explained by priming of perceptual states

Next, we wanted to clarify mechanisms behind observed transformation priming. Specifically, we wanted to confirm that prior knowledge about physical transformations is gathered in addition to and independent of the similar information on physical states (Burr & Cicchini, 2014; Cicchini, Anobile, & Burr, 2014; Fischer & Whitney, 2014).

To this end, we compared conditional probabilities for pairs of trials with same history of transformations (stability or change) but *opposite history of perceptual states*, to test a causal relationship between perception of states and perception of transformations (Pearl, 2009), see Fig. 5A. If priming is caused by prior history of perceptual states, it should be evident only for pairs of trials with a particular history of perceptual states, but absent or even reversed for the pairs of trials with opposite history. Conversely, if we observe priming for both pairs of trials, this indicates that two are independent.

For SFM, pairs of trials were sorted based on whether the initial directions of illusory rotation were the same (*congruent*) or different (*incongruent*) in both trials. For SFS, pairs of trials were sorted based on whether the initial location of light was less than 90° apart (*congruent*) or more than 90° apart (*incongruent*) in both trials.

We found that for both displays priming was present for both *congruent* and *incongruent* categories (Fig. 5B–E). For SFM (Fig. 5E), priming for *congruent* pairs $t(17) = 3.9$, $p = 0.001$; for *incongruent* pairs $t(17) = 2.8$, $p = 0.013$; the difference in priming strength was not significant $t(17) = -0.7$, $p = 0.51$. For SFS (Fig. 5B–D), priming for *match* pairs $t(8) = 7$, $p = 0.0001$; for mismatch pairs $t(8) = 7.3$, $p < 0.0001$; the difference in priming strength was not significant $t(8) = 1.9$, $p = 0.09$. Therefore, we conclude that although priming of perceptual states can stabilize perception (Burr & Cicchini, 2014; Cicchini et al., 2014; Fischer & Whitney, 2014), prior knowledge about physical transformations is gathered in addition to and independent of it.

3.4. Transformation priming cannot be explained by selective attention

Next, we considered whether repetition priming of transformations can be explained by selective attention. To this end, we reanalyzed the data of (Stonkute, Braun, & Pastukhov, 2012), where attention was distracted in every trial by a concurrent task at the time of the sudden change in the planar motion of an SFM display (see Fig. 6A and Stonkute et al. (2012) for details). This effectively precluded observers from exerting any sort of volitional control over how they perceived changes in the SFM display in individual trials, also ruling out attention to features/objects, parts/wholes, etc. In spite of this rather drastic manipulation, priming of perceptual transformations was just as strong with poor attention as with full attention ($\Delta P = 0.39 \pm 0.13$ vs. $\Delta P = 0.33 \pm 0.12$, respectively, $t(4) = 0.2$, $p = 0.53$, paired sample *t*-test, see Fig. 6B, C and Experiments 4–5 in Stonkute et al. (2012)). We conclude that priming of perceptual transformations is not the product of volitional control, nor a bias mediated by selective visual attention.

3.5. Experiment 3. Specificity of transformation priming

Finally, we wondered whether prior knowledge about transformations is gathered and exploited by a central mechanism

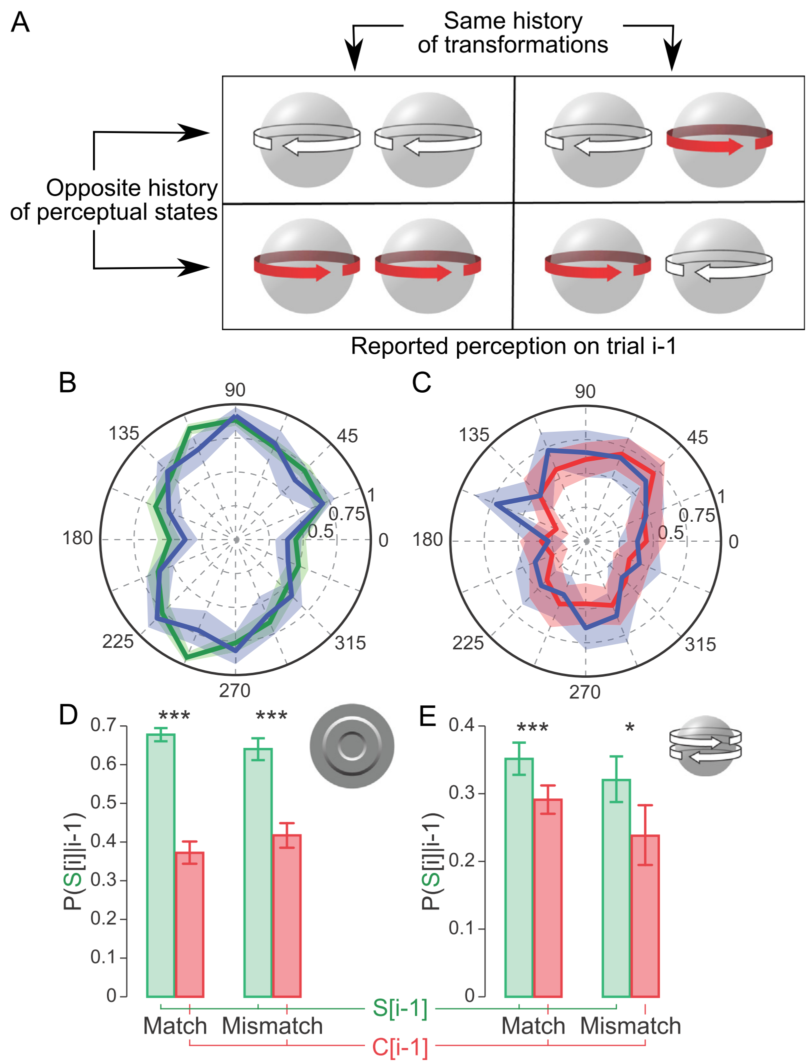

Fig. 5. Repetition priming of perceptual transformations is independent of priming of perceptual states. (A) Pairs of successive trials can be sorted based on transformations (stability/change) reported during the preceding trial (left vs. right column), or based on reported perceptual states (top vs. bottom row). If transformation priming reflects history of perceptual states, it should be evident only for top but not for bottom row trials (or vice versa). (B–D) SFS display. Successive pairs of trials i and $i-1$ were sorted by the initial location of the light source: difference of less than 90° making *congruent* pairs and difference of more than 90° making *incongruent* pairs. (B) Conditional probability of stable light given that light remained stable on the previous trial for *congruent* (green) and *incongruent* (blue) trial pairs. (C) Conditional probability of stable light given that light changed its location on the previous trial for *congruent* (red) and *incongruent* (blue) trial pairs. (D) Same as (B) and (C) but averaged over all orientations. (E) SFM display. Conditional probability of stable rotation $P(\mathrm{S}[i]|i-1)$, given the outcome of the previous trial $i-1$, for *congruent* and *incongruent* trial pairs. Successive pairs of trials i and $i-1$ were sorted by the initial direction of illusory rotation: identical directions making *congruent* (top row in A) and different directions making *incongruent* pairs (bottom row in A). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

or is represented and updated locally. To this end, we used the SFM display in conjunction with a selective adaptation procedure (Pastukhov, Füllekrug, & Braun, 2013; Pastukhov, Lissner, & Braun, 2014) to examine how priming strength is affected by a change in the stimulus location, axis of rotation, or shape (see Fig. 7A). In all cases priming from a temporally proximal (lag 1) but altered display was weaker than priming from a temporally distal (lag 2) but identical one (see Fig. 7B–D). This evidence speaks against an idea of a central mediator and suggests that perceptual inference about transformations is guided by multiple contemporaneous memories of recent perceptual choices.

4. Discussion

We investigated the general mechanism with which our vision resolves dynamic ambiguities of sudden changes in retinal input. To this end, we employed three disparate visual displays, where a sudden change in sensory inputs produced perception of ambiguous transformations. We observed a reliable repetition priming of transformations: the same perceptual interpretation of change in sensory evidence tended to be repeated on consecutive trials. The transformation priming in question was contingent on earlier perceptual experience and depended neither on priming of perceptual states, nor on selective visual attention.

Our results provide further evidence for the importance of prior knowledge about physical transformations for the visual system by showing that it gathers the information from recent *perceived* changes to update prior knowledge about *physical* ones. Critically, this repetition priming was observed for three disparate displays, whose perception relies on distinct neural representations. In addition, the specificity of priming speaks against a notion of a central mediator, but in favor of a locally implemented canonical mechanism. Taken together this suggests that both knowledge about physical transformations and its dynamic update reflect an overall adaptive strategy of the visual system and are an integral part of a general perception. Accordingly, the influence of dynamic prior

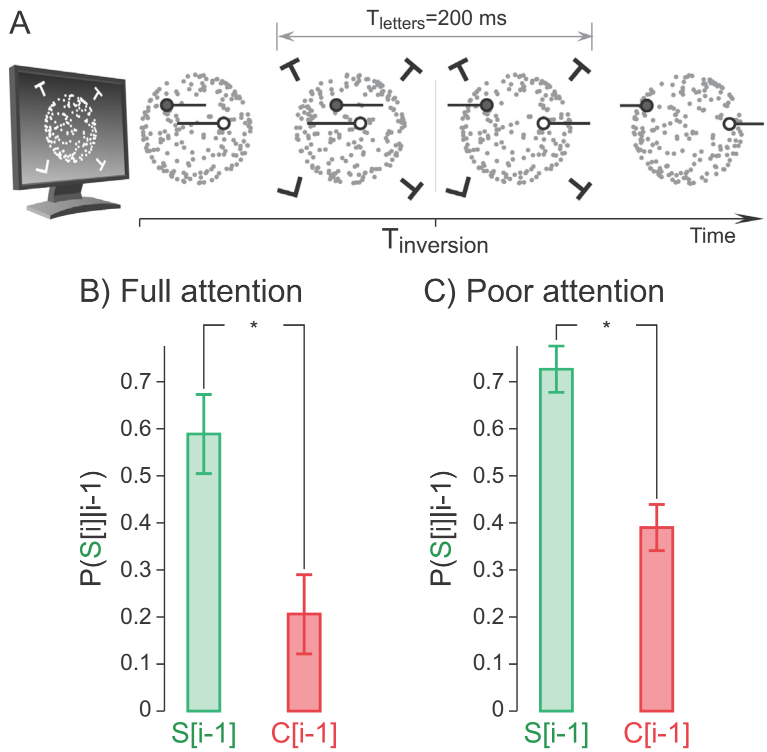

Fig. 6. Priming of perceptual transformations in structure-from-motion (SFM) displays is independent from attention. (A) Schematic procedure. In addition to the illusory SFM sphere, an attention-demanding letter task was presented around the SFM object for 200 ms, bracketing time of the physical motion reversal. Observers reported on (1) the letter-task alone (control condition), (2) the perceptual stability of the SFM sphere alone (full attention condition), (3) first on the letter-task, when on the perceptual stability of the SFM sphere (poor attention condition). See Stonkute et al. (2012) for details. (B) In full attention condition, strong priming of perceptual transformations replicated results of the Experiment 1a. (C) Similarly strong priming was observed in poor attention condition, showing that priming of perceptual transition is independent of attention.

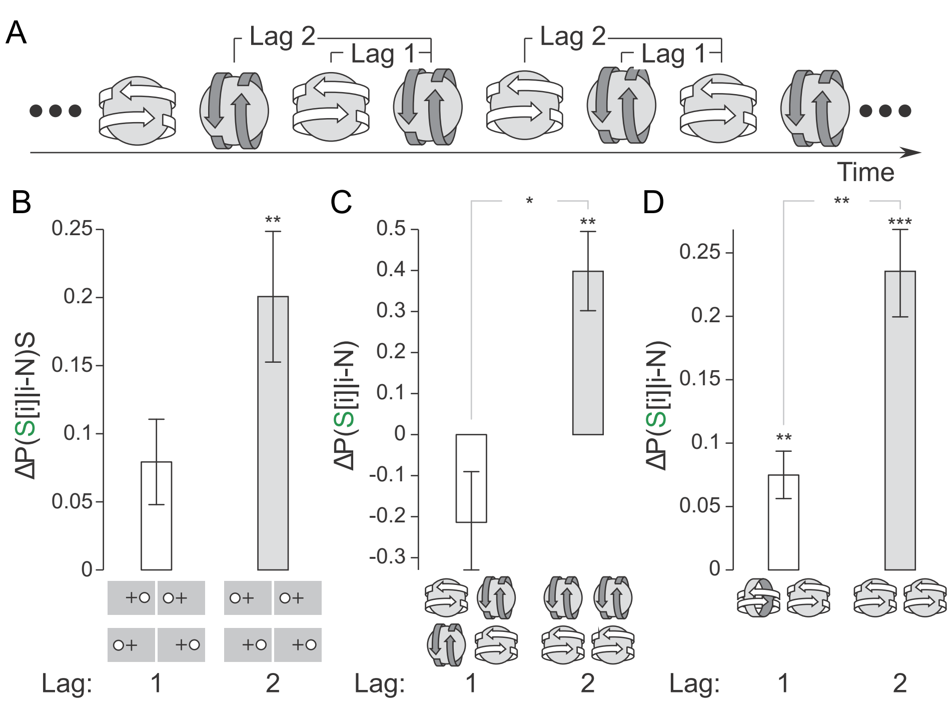

Fig. 7. Experiment 3. Changes to the display reduced priming of perceived transformations. (A) Schematic procedure. Two alternative versions of the SFM display were presented repeatedly and intermittently. (B) Priming of perceived transformations was reduced by change in the stimulus location. Same location $\Delta P = 0.2 \pm 0.05$, $t(5) = 4.2$, $p = 0.008$; at different locations $\Delta P = 0.08 \pm 0.03$, $t(5) = 2.5$, $p = 0.053$; difference was marginally insignificant $t(5) = -2.4$, $p = 0.06$ (all comparisons here and below were paired-sample t-tests). (C) Priming was reduced by change in the axis of rotation. Same axis $\Delta P = 0.4 \pm 0.1$, $t(5) = 4.1$, $p = 0.009$; orthogonal axes $\Delta P = -0.2 \pm 0.12$, $t(5) = -1.8$, $p = 0.14$; difference was significant $t(5) = -2.9$, $p = 0.035$. (D) Priming was reduced by change of object's shape. Same object $\Delta P = 0.23 \pm 0.03$, $t(7) = 6.8$, $p = 0.0002$; different object $\Delta P = 0.08 \pm 0.02$, $t(7) = 4$, $p = 0.005$; difference was significant $t(7) = -4.9$, $p = 0.002$.

knowledge must be taken into account when studying dynamic visual scenes.

The need for this general mechanism, which helps to disambiguate changes, comes from the environment we inhabit. The outside world is highly dynamic with constant changes due to both observer self-motion (attention shifts, eye movements, blinks, locomotion) and dynamical processes in the environment (object motion, deformation, occlusion, changes in illumination, and so on). Sudden visual changes are not only ubiquitous but presents a particular challenge, as the retinal trace is brief and the number of alternatives is typically large. Thus, the visual system must decide on very slender evidence whether a change in the retinal input reflects an actual physical change in the outside world and what kind of transformation has occurred. In signal detection terms the visual system must set a criterion that is neither too conservative (as too many actual changes would be missed), nor too liberal (as too many detected changes would be spurious). In part, the visual system uses context to find a criterion to balance sensitivity and stability (Kawabe & Miura, 2006; Stonkute et al., 2012; Wexler et al., 2001). In part, it relies on prior knowledge about the physical plausibility (or implausibility) of a particular change that governs both detection (Pastukhov et al., 2012; Stonkute et al., 2012; Treue, Andersen, Ando, & Hildreth, 1995) and appearance (Barbur & Spang, 2008; Combe & Wexler, 2010; Suzuki & Grabowecky, 2002; Tse, 2006; Tse & Logothetis, 2002; Wexler et al., 2005) of transformations. Transformation priming appears to provide an additional mechanism for adjusting the criterion dynamically to the current visual environment on the basis of recent perceptual experience.

To see how dynamically adjusted transformations prior can work in addition to priors of appearance, it helps to visualize the hypothesized internal dynamics of perception in terms of a landscape of "effective energy". This "energy landscape", within which collective neural activity unfolds, is formed by visual representations (Braun & Mattia, 2010; Kelso, 2012). Specific phenomenal appearances are implemented as energy valleys ("attractor states"), whose "depth" reflects both sensory evidence and prior knowledge. Within this framework, "transformation priors" could be instantiated straightforwardly as ridges ("transition energies") between selected valleys. In turn, transition priming would modulate the "height" of ridges, reflecting earlier perceptual experience. A successful transition to a different state would lower it, facilitating future transitions *in both directions*, making transformation priming independent from priming of states (Fig. 8A). Conversely, evidence about perceptual stability would increase

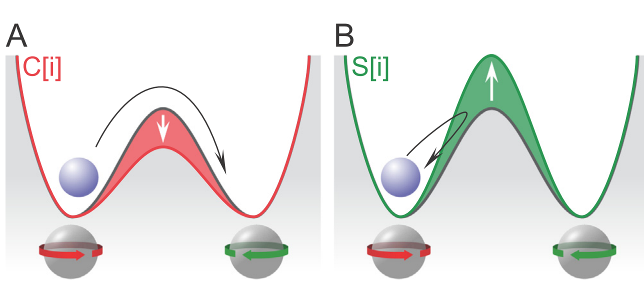

Fig. 8. Transformation priming visualized in terms of an "effective energy" landscape. For multi-stable displays the "effective energy" landscape contains two adjacent energy wells that correspond to two favored perceptual states. The ridge in-between determines energy required for a perceptual alternation to occur. Changes in sensory evidence and fluctuations in spontaneous activity may push perception (depicted as a blue ball) towards an alternative state (black arrow). (A) A recent experience of a perceptual transformation increases its likelihood by lowering the ridge. (B) Conversely, a failed attempted reversal raises the ridge, decreasing a likelihood of this transformation in the future. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

required transition energies, preventing transitions also from *both* perceptual states (Fig. 8B).

Our results build upon prior research, such as work on "perceptual trapping" (Suzuki & Grabowecky, 2007), pattern completion mechanisms (Denison, Piazza, & Silver, 2011; Maloney, Dal Martello, Sahm, & Spillmann, 2005), and speeding of perceptual alternations (Pastukhov & Braun, 2013a; Suzuki & Grabowecky, 2007), which had already hinted that the influence of a recent experience may go beyond priming of specific perceptual states. Here we conclusively demonstrate priming specific to recent experience of perceptual transformations, rather than to recent perceptual states. We also show that it is independent of selective attention. Whereas in the present experiments priming lasted for seconds, other effects induced by recent experience, which may be linked to perception of transformations, retain their influence over far longer time-scales (Klink, Brascamp, Blake, & van Wezel, 2010; Pastukhov & Braun, 2013a; Suzuki & Grabowecky, 2007). Moreover, priming of perceptual states exhibits both facilitatory (Leopold et al., 2002; Orbach, Ehrlich, & Heath, 1963; Pastukhov & Braun, 2013b; Pastukhov, Füllekrug, et al., 2013; Pastukhov, Lissner, Füllekrug, et al., 2014) and inhibitory effects (Pastukhov & Braun, 2011, 2013b) operating concurrently on different time-scales. Similarly diverging effects may also exist for priming of transformations. A possible instance of such a divergence is the perceptual stabilization over single sessions combined with "speeding" of perceptual alternations over days reported for multi-stable displays (Pastukhov & Braun, 2013a; Suzuki & Grabowecky, 2007). Thus, further studies may well reveal several additional layers of complexity in priming of transformations by recent perceptual experience.

Although reported priming of transformations is independent of history of perceptual states (see Section 3.3), it works alongside multiple state-oriented mechanisms that balance conflicting goals of maintaining perceptual constancy while ensuring sensitivity to changes in sensory inputs. For example, perceptual adaptation is thought to prioritize perceptual sensitivity (Kohn, 2007; Pastukhov, García-Rodríguez, et al., 2013; Theodoni, Kovács, Greenlee, & Deco, 2011; Webster, 2011). Conversely, neural persistence (Coltheart, 1980; Loftus & Irwin, 1998; Pastukhov & Braun, 2013b) and a rolling average over a longer period of perceptual history are thought to be used to minimize influence of neural noise and ensure perceptual constancy (Burr & Cicchini, 2014; Cicchini et al., 2014; Fischer & Whitney, 2014). Finally, several mechanisms work as predictive memories trying to optimize target selection and processing (Chopin & Mamassian, 2012; Grill-Spector, Henson, & Martin, 2006; Kristjánsson & Campana, 2010; Maljkovic & Nakayama, 1994, 2000; Schacter, Dobbins, & Schnyer, 2004). Accordingly, future studies should focus not only on individual mechanisms (whether state- or transformation-oriented) but on their interaction in perception.

5. Conclusions

We report a phenomenon of repetition priming of transformations. Our results demonstrate that this is a general perceptual phenomenon and suggest that priming by recent experience is considerably more selective and detailed than hitherto appreciated.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.visres.2015.09.005.

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