Brain state and changes of mind: Probing the neural bases of multi-stable perceptual dynamics
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Chapter 4

Short-term Stabilization in Bistable Visual Perception

This chapter is based on:
ABSTRACT

In bistable perceptual illusions, perception alternates spontaneously and unpredictably between distinct interpretations of a constant sensory stimulus. Distributions of percept durations reported by psychophysical observers in these illusions are typically asymmetric, with a rapid growth and a long tail. Remarkably, the mode (most frequent percept duration) and shape of the distributions vary widely across individuals, while being highly reproducible within individuals. What causes these individual differences? Specifically, observers typically report only very few percepts that are shorter than their mode. Here, we explored two alternative scenarios that could explain the lack of very short percepts.

In the first scenario, observers do in fact experience these short percepts, but some are better able to accurately track and report them than others (motor latency scenario). Alternatively, observers might experience a genuine lack of short percepts, indicating that perception briefly stabilizes after a perceptual switch (perceptual stabilization scenario).

Both these scenarios could result in the observed individual differences in percept duration modes. To arbitrate between them, we asked 33 observers to report perceptual switches during two bistable visual illusions (Motion-Induced Blindness and Structure-from-Motion) as well as during a physical replay of these illusions containing percept durations reported by the fastest switching (“reference”) observer. We found that all observers were well able to accurately report percept durations shorter than their mode reported during the illusion, supporting the perceptual stabilization scenario. Thus, our results suggest a stabilizing mechanism preventing immediate return transitions during bistable visual illusions, which varies in strength across individuals. Such stabilization might occur through a combination of sensory adaptation and active top-down modulation of neural activity.

Keywords: bistable perception, psychophysics, individual differences
INTRODUCTION

Perception sometimes alternates spontaneously between distinct interpretations of the same sensory input, a phenomenon referred to as bistable perception (Blake and Logothetis, 2002; Deco and Romo, 2008). For example, in “motion-induced blindness” (MIB) (Bonneh et al., 2001; Donner et al., 2008; Bonneh and Donner, 2011; Donner et al., 2013; Bonneh et al., 2014), a salient visual target spontaneously disappears when surrounded by a moving mask, only to re-appear after some period of time. In “3D-structure-from-motion” (SfM) (Klink et al., 2008) a cloud of dots is perceived as a sphere rotating around its vertical axis. When viewing this stimulus for an extended period of time, the perceived direction of rotation alternates spontaneously. Different bistable perceptual phenomena are governed by common dynamical principles (Brascamp et al., 2006; Klink et al., 2008; Bonneh et al., 2014).

Computational models of bistable perception posit that the spontaneous perceptual dynamics result from intrinsic (independent of stimulus changes) fluctuations in the activity of stimulus-selective populations of neurons (Blake and Logothetis, 2002; Laing and Chow, 2002; Wilson, 2003; Freeman, 2005; Kim et al., 2006; Moreno-Bote et al., 2007; Noest et al., 2007; Gigante et al., 2009; Pastukhov et al., 2013). These intrinsic activity fluctuations emerge from the interplay of random fluctuations (“noise”) of neuronal activity and competitive interactions between neuronal populations processing the distinct stimulus features (Moreno-Bote et al., 2007; Donner et al., 2013; van Loon et al., 2013). In the absence of any mechanism promoting the stability of a given perceptual dominance state, neuronal competition models of bistable perception predict exponentially distributed durations of perceptual dominance states (Moreno-Bote et al., 2007) (see Figure 1A, gray line, for an example). By contrast, the percept duration distributions reported by psychophysical observers are asymmetric, with a rapid growth and a long tail (see Figure 1A, black line, for an example), often modeled as a gamma distribution (Leopold and Logothetis, 1999). Remarkably, the center of mass (typically quantified by the mode) and shape of the percept duration distribution vary widely across individuals, while being highly reproducible within individuals (Leopold and Logothetis, 1999; Donner et al., 2013; van Loon et al., 2013).

What causes the individual differences in the perceptual dynamics? More specifically: what causes the individual differences in the center of mass of the percept
duration distributions? Here, we explored two alternative scenarios. First, observers, in fact, experience many short percepts (corresponding to the gray distribution in Figure 1A) but some are better able to report them behaviorally than others. In other words, the individual differences in the center of mass reflect different latencies of motor response (typically button presses). In the following we refer to this scenario as “motor latency”. Alternatively, the individual differences in the center of mass reflect actual differences in the perceptual dynamics due to a mechanism that stabilizes the newly selected percept for some time, thereby preventing rapid return transitions. When this short-term stabilizing mechanism has a strong effect, the observer only rarely experiences short percepts. In the following, we refer to this scenario as “percept stabilization”. Note that the term is neutral with respect to the underlying mechanism: it comprises both local adaptation (Blake et al., 2003; Noest et al., 2007) as well as active (“top-down”) forms of stabilization (Leopold et al., 2002; Einhauser et al., 2008; Kloosterman et al., 2014).

The goal of the present study was to arbitrate between the motor latency and the percept stabilization scenarios, to shed light on the origin of individual differences in bistable perception. To this end, we asked observers to report their alternations of perception in two conditions: (i) during a bistable visual illusion (MIB or SfM); and (ii) during a sequence of physical stimulus changes, which evoked perceptual alternations that
resembled those in the illusions in terms of their phenomenal appearance, but occurred more rapidly than the alternations they reported during the illusions. This was achieved by replaying the spontaneous perceptual alternations reported during the illusions by the observer who exhibited the fastest perceptual dynamics in our sample of observers. We, henceforth, refer to this observer as the “reference observer” and to condition (ii) as the “Fast Replay” and contrast it with the “corresponding illusion”, i.e., condition (i). The “Fast Replay” condition eliminated the effect of a possible percept stabilization mechanism (due to the presentation of salient physical stimulus events) and thereby isolated the effect of motor (report) latency.

The “Fast Replay” condition elicited a large fraction of short percepts (i.e., more akin to the gray than to the black distribution in Figure 1A), while still allowing for accurate behavioral report by at least one observer within our sample (the reference observer). If the differences in center of mass between the reference observer and the other observers were determined by longer motor latencies, then the other observers should not be able to track the Fast replay alternations with their behavioral reports. In other words, the center of mass in the Fast replay should be more similar to each observer’s own center of mass in the corresponding illusion than to the center of mass of the reference observer (Figure 1B, left). In contrast, if the individual differences in the center of mass were determined by differences in percept stabilization, then each observer’s center of mass in the Fast replay should be more similar to the center of mass of the reference observer (Figure 1B, right). Our results support the second scenario.

MATERIALS AND METHODS

Subjects

33 observers (20 female, age range: 18 - 35 years) participated in the experiment. All observers had normal or corrected-to-normal vision and gave written informed consent. The experiment was conducted in two groups of observers. One group (N = 10) performed the illusion and Fast replay conditions with only the MIB stimulus. The other group (N = 23) performed both conditions with both the MIB and the SfM stimuli. Two observers of this group were excluded due to not responding at all in at least two trials. Thus, 21 observers of this group were entered in the analysis. The experiment was approved by
the ethics committees of the Department of Psychology at the University of Amsterdam and the VU University Medical Center, Amsterdam.

**Stimuli**

*MIB illusion*

The ten MIB-only observers viewed an MIB stimulus consisting of a yellow target and a blue mask on a black background (Figure 2A). The target was a salient yellow disc (full contrast, diameter: 0.12 or 0.2° of visual angle) surrounded by a moving mask (square, equally spaced grid of 9 by 9 blue crosses, 17° width/length), both superimposed on a black background and centered on a fixation mark (red outline, white inside, 0.8° width and length) (Figure 2A, left). The target was located on one of the four visual field diagonals at an eccentricity of 3°. Target size and location (visual field quadrant) were individually selected for each subject prior to the experiment, to yield a percentage of target invisible time of at least 20%. The mask rotated around the fixation square (speed: 120°/s). The target was separated from the mask by a black “protection zone” subtending about 2° around the target (Bonneh et al., 2001). Stimuli were presented using the Presentation Software (NeuroBehavioral Systems, Albany, CA, USA).

During the illusory MIB condition, observers were supinely placed in a whole-head magneto-encephalography (MEG) scanner setup (Elekta Neuromag Oy, Helsinki, Finland). The MEG data are reported in Chapter 2 (Kloosterman et al., 2014). The stimulus was projected via two mirrors onto the ceiling of the MEG scanner room by an LCD projector (BarcoData 8200 LC, Barco Projection Systems, Kuurne, Belgium) with a pixel resolution of 800 × 600 and 60 Hz refresh rate (field of view of 18 × 23°).

The 21 MIB-and-SfM observers viewed the same MIB stimulus during the illusory condition as described above, with the following exceptions: the target was a black-and-white Gabor patch (diameter: 2°; location: 5° eccentricity in one of the four visual field quadrants), the mask was white and the stimulus background was gray.

*SfM illusion*

The SfM stimulus consisted of an array of black and white dots (dot diameter: 0.1°), centered on a fixation circle (red outline, green inside, 0.5° diameter) in the middle of a gray screen and limited to a circular aperture (diameter: 10°) (Figure 2A, right). The
A

**MIB**

Button state:
- Mapping 1: Up, Down
- Mapping 2: Up, Down

**SfM**

Button states:
- Button 1: Up, Down
- Button 2: Up, Down

**Percept:**
- or

**Physical stimulus:**
- Target

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B

**MIB**

Button state:
- Up, Down

**SfM**

Button states:
- Button 1: Up, Down
- Button 2: Up, Down

**Percept:**
- or

**Physical stimulus:**
- Target
coordinated movement of the dots on the x-, y- and z-axes on a two-dimensional plane created the impression of a three-dimensional sphere rotating around its vertical axis. The peak dot velocity was in the center of the sphere and decreased towards the edges. The perceived rotation direction of the sphere was bistable, such that a constantly moving stimulus gave rise to an alternating subjective perception of left- and rightward rotation.

The 21 MIB-and-SfM observers were seated in a silent and dimly lit room, 50 cm in front of the computer screen. Stimuli were displayed on a 32-bit LaCie Electron Blue 4 CRT monitor with a resolution of 1024x768 pixels at a refresh rate of 85 Hz. Observers were seated in a silent and dark room, with their head positioned on a chin rest, 50 cm in front of the computer screen. During the experiment, the left eye was tracked at 1000 Hz with an average spatial resolution of 15 to 30 min arc, using an EyeLink 1000 697 Desktop Mount (SR Research, Osgoode, Ontario, Canada). The eye tracking data are not reported in this chapter.

Fast replay

During the Fast Replay conditions, observers reported their perception of a sequence of physical stimulus changes that mimicked the phenomenal appearance of the illusions (MIB, SfM) (Figure 2B), but were, for all but one observer (the reference observer), faster than the spontaneous perceptual alternations reported during the illusions. This sequence was a replay of the spontaneous alternations reported by the one observer who reported the fastest alternations during the illusions. We selected the observer with the highest
switch rate as the reference observer, defined as the total number of switches divided by the total stimulus duration) (Figure 3A and B, thick black line).

Perceptual switches during Fast replay of MIB were evoked by actual onsets and offsets of the target on the screen. This sequence was a replay of illusory target disappearances and re-appearances reported by the reference observer. The same reference observer was used for the ten MIB-only and the 21 MIB-and-SfM observers. The target viewed by the MIB-only observers during Fast replay was identical to the target used during the corresponding MIB, but enlarged (4° of visual angle) to minimize the occurrence of illusory target disappearances due to MIB. The Fast replay MIB stimulus was displayed on a 22 inch LCD monitor (Asus VW222U) with a resolution of 800x600 pixels at a refresh rate of 60 Hz. Observers were seated in a silent and dark room during this condition.

The Gabor target viewed by the MIB-and-SfM observers during Fast replay of MIB was initially the same size as during the illusory MIB condition. Thus, observers were not able to visually track the target offsets and onsets during Fast replay due to MIB (data not shown). Twelve of the 21 observers of this group were available for an extra session, in which they performed the Fast replay again, but now with a bigger target (4° of visual angle). In Figure 3A and B, left panels, we report the data of these twelve observers combined with the ten MIB-only observers. Both groups analyzed separately show the same qualitative results (data not shown). In Figure 3A and B, right panels, we report the data of the SfM illusion and its Fast replay for all 21 MIB-and-SfM observers that initially performed the experiment. In Figure 4, we also report the illusory conditions of all MIB-and-SfM observers.

During the Fast replay of SfM, the ambiguity of the sphere's rotation direction was resolved by decreasing the luminance, contrast and size of each dot as a function of its location on the z-axis (depth). Reversing the presentation order of the array of frames evoked alternations in perceived rotation direction.

**Task and procedure**

The ten MIB-only observers performed the MIB condition and its Fast replay over three days: MIB (days 1 and 2), followed by Fast replay (day 3). During MIB, observers reported the spontaneous disappearance and re-appearance of the target by pressing or releasing
a response button with their index finger (left or right, counterbalanced across observers). The mapping between perceptual switch and motor response was flipped between the two recording days (Figure 2A, top left): button press for indicating target disappearance (release for re-appearance) on day 1, and button release for disappearance (press for re-appearance) on day 2. During Fast Replay, observers continuously depressed the space bar on a keyboard when the target was removed from the screen and released it when the target was replaced. Observers completed 32 runs of 2 min duration of MIB and twelve runs of Fast Replay.

The 21 MIB-and-SfM observers indicated their current percept during the MIB and SfM illusion and corresponding Fast replay by pressing the “.” or “/” button on a keyboard with their index or middle finger respectively. The mapping between perceptual switch during MIB (disappearance, re-appearance) and motor response was counterbalanced across observers. During SfM, these observers continuously reported the spontaneous or stimulus-evoked alternations of perceived rotation direction. All observers reported leftward rotation with their right index finger, and rightward rotation with their right middle finger. Observers completed ten runs of 2 minutes for the illusory conditions and 5 runs of 2 minutes for Fast replay in randomized order. Observers performed the MIB and SfM conditions in two distinct blocks. Block order was counterbalanced across observers. Twelve of the 21 observers performed an extra session in which they performed Fast Replay of MIB with a bigger target (see Fast replay section).

**Data analysis**

The aim of our analyses was to quantify and compare the centers of mass of observers’ percept durations during the MIB and SfM visual illusions and their corresponding Fast replay conditions. We defined the center of mass as the mode percept duration. We extracted the mode for each subject and condition by first binning the percept durations (see below for bin sizes used) and selecting the most often-occurring duration. If there were multiple percept durations occurring equally frequently, we selected the smallest of those values as the mode. Thus, the mode corresponds to the first peak in the frequency distribution of percept durations (indicated by crosses in Figures 1B, 3A and 3B). We normalized distributions within each subject by dividing the number of occurrences in each bin by the total number of switches reported by the subject.
Similarity between percept duration distributions from illusion and Fast Replay

As a measure of overall similarity between percept duration distributions during illusions and Fast replay plotted in Figure 3A, we computed the Pearson correlation between each subject’s Fast replay percept duration distribution and (i) their own percept duration distribution for the illusion and (ii) the percept duration distribution of the reference observer (Figure 3C). Due to the generally shorter percept durations in MIB than in SfM, we used bin sizes of 0.1 s for MIB and 0.5 s for SfM, respectively, as well as their corresponding Fast Replay. We tested whether the two correlations, averaged across observers, were significantly different using a permutation (shuffling) procedure (see Statistical comparisons).

Similarity of center of mass during illusion and Fast Replay

The motor latency scenario predicts that each observer’s mode percept duration during Fast replay is more similar to their mode in the corresponding illusion than to the reference observer’s mode (Figure 1B, left). The percept stabilization scenario predicts the opposite (Figure 1B, right). To test these predictions, we computed for each subject the mode percept duration during the illusory conditions and their corresponding Fast replay and statistically tested these modes against each other across observers using a permutation procedure (see Statistical comparisons). We used bin sizes of 0.025 s for MIB and 0.25 s for SfM and its corresponding Fast replay for computing the mode.

Correlation between median percept durations across illusions

To test whether observers produced similar perceptual dynamics across different bistable illusions, we pooled within each subject all percept durations of the MIB and SfM illusions in Experiment 2 and computed the median. We then Pearson-correlated these median durations across observers and tested significance of the correlations with a permutation procedure (see Statistical comparisons). We used the median instead of the mode or mean in this analysis, because the median captures the typical percept duration better than the mode or mean due to the skewedness of percept duration distributions. In addition, the median is less sensitive to outliers than the mean.
Statistical comparisons

We used two-tailed non-parametric permutation procedures across observers (Efron and Tibshirani, 1998) for testing significance of the correlation between illusion and Fast replay distributions against the correlation between Reference and Fast replay distributions (Figure 3C), as well as testing the modes during the illusory conditions against the Fast replay modes (Figure 3D). All statistical tests were performed across observers. For each comparison, we randomly permuted the labels of the observations (e.g., the condition labels of mode percept durations), and recalculated the difference between the two group means (1000 permutations). The p-value associated with the original difference between the means was given by the fraction of shuffles in which the original difference was exceeded by the difference between the means obtained for the shuffled data.

RESULTS

All observers, including those with the slowest spontaneous perceptual dynamics (i.e., a mode of several seconds longer than the one of the reference observer), were able to accurately report the rapid stimulus alternations during Fast replay of both the MIB and SfM illusions (Figure 3). In other words, the observers produced percept duration distributions that closely resembled the distribution produced by the reference observer during the illusory condition (black lines Figure 3A and 3B) and not their own illusory distribution (Figure 3A).

We used Pearson correlation to quantify the overall similarity of observers’ percept duration distributions from the Fast replay with both the reference distribution and their own distribution during the illusion. For both MIB and SfM, there was a significantly stronger correlation between each subject’s Fast replay distribution and the distribution of the reference subject than between Fast replay and the subject’s own illusory distribution (MIB, p = 0.008; SfM, p < 0.001; Figure 3C). Thus, observers’ Fast replay distributions were more similar to the reference observer’s distribution than to each observer’s own illusory distributions.

We then tested the key prediction of the percept stabilization scenario: that each observer’s center of mass (defined as the mode percept duration) during Fast replay would be more similar to the center of mass of the reference observer than to their own
Figure 3 | Lack of short percepts is not explained by motor latency

A. Frequency distributions of percept durations reported during the illusory conditions Left, MIB (target disappearance). Data are collapsed over the two types of MIB stimuli (N = 21 observers). Right, SfM (left and right rotation percepts pooled). Thick black lines, distribution of the reference observer, which was used for generating the sequence of stimulus alternations in the Fast replay conditions. Crosses above distributions, mode percept durations of single observers and reference observer (bold). Inset, SfM distribution averaged across observers, showing the long tail of the distribution. B. Percept duration distributions for button states during Fast Replay. The distributions match the ones predicted under percept stabilization. C. Correlations between observers’ own illusory distributions and their Fast replay and between the reference observer’s distribution and their Fast Replay. *, p < 0.05, **, p < 0.01, ***, p < 0.001. Error bars, s.e.m. D. Mode percept duration averaged across observers during MIB and SfM and corresponding Fast Replay. Dotted line, mode percept duration of the reference observer.

center of mass in the corresponding illusion. This is indeed what we found: for both MIB and SfM, the average mode across observers during Fast replay was significantly closer to the mode of the reference observer than to the average mode during the illusion (MIB, p < 0.001, SfM, p = 0.004; permutation tests across observers) (Figure 3D). There was significant difference between the mode produced during Fast Replay and the mode of the reference observer (MIB, p = 0.57, SfM, p = 0.39). Taken together, our results indicate that observers were in fact well able to report shorter percept durations than they typically do during bistable illusions.

Finally, we assessed whether individual differences in the perceptual dynamics (specifically: the median percept duration) are correlated between different bistable illusions. To this end, we correlated the median perceptual dominance durations observed in MIB to those observed in SfM across observers and found a significant positive correlation (r = 0.48, p = 0.02, permutation test) (Figure 4), indicating that observers who generally experience longer percepts in one illusion, also have longer percepts in another illusion. In other words, the perceptual state dynamics do not only differ markedly across individuals, but they are also highly consistent across different phenomena within an individual.

DISCUSSION

Here, we assessed the origin of the large individual differences in the dynamics of bistable visual perception. In the absence of any mechanism stabilizing the newly selected perceptual state (Moreno-Bote et al., 2007), the only factor limiting the report of very short percepts is the inability to track these short percepts by means of behavioral reports
(motor latency). In contrast, our current results show that all observers were well able to report percepts much shorter than their own mode percept duration during two different illusions. This result is independent of the specific type of motor regime (using one or two response buttons, Figure 2) that observers use to indicate perceptual switches. In sum, noise and motor latency combined are not sufficient to explain the reported perceptual dynamics. Thus, our results are consistent with the existence of a stabilizing mechanism that prevents immediate return transitions during bistable visual illusions.

What is this stabilizing mechanism? Adaptation of stimulus-selective sensory neurons is one candidate (Noest et al., 2007). When combined with noise and competition, adaptation can qualitatively re-produce the empirically observed asymmetric percept duration distributions (Moreno-Bote et al., 2007). Indeed, there is paramount evidence for the effects of adaptation in primate visual cortex (Kohn, 2007) and there is fMRI evidence for a role of target-specific neuronal dynamics in human V1 (presumably linked to adaptation) in the stability of MIB target disappearance (Donner et al., 2013). Notably, adaptation predicts some degree of history-dependence in the perceptual dynamics (i.e., correlation between the duration for which a percept is suppressed and the following period in which it is dominant) (Leopold and Logothetis, 1999; Pastukhov et al., 2013), which is subtle in empirical data (Pastukhov and Braun, 2007; van Ee, 2009). While the existence of stimulus-selective adaptation mechanisms in visual cortex is unquestionable, it remains to be seen whether their effects are sufficiently strong and variable across people to account for the striking individual differences in the perceptual dynamics in bistable visual illusions.

\[ \tau_A \partial A_i = -A_i + \alpha S[X_j], \]
\[ i, j \in \{1, 2\} \]
Another candidate is an active top-down mechanism triggered by the perceptual switch (Einhauser et al., 2008; Kloosterman et al., 2014). Indirect evidence from pupillometry shows a correlation between pupil dilation during perceptual switches and the duration of the newly selected perceptual state (Einhauser et al., 2008). Based on the putative link between pupil dilation and brain-wide noradrenaline release (Aston-Jones and Cohen, 2005), this finding could be interpreted as evidence for a role of noradrenergic neuromodulation in perceptual stabilization. During MIB, transient modulations of beta-band activity in visual cortex around perceptual report of target disappearance also predict the duration of the subsequent MIB state (Kloosterman et al., 2014). Finally, the phenomenon of protracted repetition of perceptual judgments during intermittent presentation of ambiguous stimuli has also been interpreted as evidence for an active stabilization mechanism (Leopold et al., 2002) (but see Noest et al. (2007)). Adaptation and top-down factors might conspire to determine the stability of a perceptual state.

It is tempting to speculate that the stabilization mechanism characterized here during bistable visual perception generalizes to higher-order thought, as well as its disturbances in psychiatric conditions. The perceptual dynamics in these illusions are altered in depression and autism (Leopold and Logothetis, 1999; Pettigrew, 2001; Robertson et al., 2013) and they resemble the dynamics of fixation durations – a proxy of the durations of individual thoughts – during challenging cognitive tasks (Suppes et al., 1983). In sum, the bistable perceptual dynamics investigated here may be a fingerprint of an individual’s general “stream of thought”. Uncovering the underlying mechanism may thus prove instrumental for understanding individual differences in the dynamics of cognition.

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