Persistent states in vision break universality and time invariance

Mark Wexler^{a,1}, Marianne Duyck^a, and Pascal Mamassian^b

^aLaboratoire Psychologie de la Perception, CNRS UMR 8242, Université Paris Descartes, 75006 Paris, France; and ^bLaboratoire des Systèmes Perceptifs, CNRS UMR 8248, École Normale Supérieure, 75005 Paris, France

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Studies of perception usually emphasize processes that are largely universal across observers and—except for short-term fluctuations—stationary over time. Here we test the universality and stationarity assumptions with two families of ambiguous visual stimuli. Each stimulus can be perceived in two different ways, parameterized by two opposite directions from a continuous circular variable. A large-sample study showed that almost all observers have preferred directions or biases, with directions lying within 90 degrees of the bias direction nearly always perceived and opposite directions almost never perceived. The biases differ dramatically from one observer to the next, and although nearly every bias direction occurs in the population, the population distributions of the biases are nonuniform, featuring asymmetric peaks in the cardinal directions. The biases for the two families of stimuli are independent and have distinct population distributions. Following external perturbations and spontaneous fluctuations, the biases decay over tens of seconds toward their initial values. Persistent changes in the biases are found on time scales of several minutes to 1 hour. On scales of days to months, the biases undergo a variety of dynamical processes such as drifts, jumps, and oscillations. The global statistics of a majority of these long-term time series are well modeled as random walk processes. The measurable fluctuations of these hitherto unknown degrees of freedom show that the assumptions of universality and stationarity in perception may be unwarranted and that models of perception must include both directly observable variables as well as covert, persistent states.

perception | vision | depth | bias | persistent state

The neural networks underlying visual perception are complex systems and, as such, undoubtedly have internal states. The formal notion of “state” can be defined as the minimal set of variables that, together with the input to a system and the fixed processing mechanisms, allows one to predict the system’s output (1). If perception is a function of both the sensory input and internal states, then—because states can vary both across individual observers and over time—the presence of an internal state would manifest itself as potentially large individual differences in the perception of the same stimulus and in coherent temporal variations of perception of the same stimulus over time in a single observer. It is known that visual functions can be modulated (2) on brief time scales by priming (3–6), aftereffects (7–9), and sequence effects (10–13) [and sometimes on larger time scales as well (14)]; can undergo visible short-term fluctuations in the presence of multistable stimuli (15–20); and can undergo long-term or permanent changes in their structure through learning (21–24). Despite these examples, little is known about internal states of the visual system. In terms of underlying mechanisms, the internal state is represented naturally in recurrent but not in feed-forward neural networks (25, 26).

Here we measure patterns of biases in two families of visual stimuli and show that, contrary to most known cases, these patterns can vary radically from one observer to the next, leading to stimuli that are often perceived in opposite ways by different observers. We show that these bias patterns can be predicted to a large extent by simple variables. We therefore call these parameters “state

variables.” They constitute a form of long-term but dynamic memory in perception and are related to but distinct from the phenomenon of short-term coherence in the perception of multistable stimuli known as sensory memory (15–20), as we discuss below.

The stimuli in the first family, which we call structure-from-motion (SFM), consist of moving dots simulating planes rotating in depth (Fig. 1A). [Examples of stimuli and response procedures for the two families of stimuli may be seen at lab-perception.org/demo/p/sfm and lab-perception.org/demo/p/tfm. Following the 16-trial session, the web page displays the participant’s bias.] Each stimulus can be perceived as having one of two tilts (27–29), separated by 180 degrees (Fig. 1B and D). The stimuli in the second family, transparency-from-motion (TFM), consist of two sets of dots moving in opposite directions (Fig. 1C). The two sets of dots are usually perceived as transparent layers, one of which is seen as being closer or more salient (30–32), also giving rise to a 180 degree ambiguity (Fig. 1D). Observers reported which of the two tilts they perceived for SFM stimuli and which of the two motion directions they perceived closer for TFM stimuli. Successive stimuli had different orientations (tilts or motion directions), sampled in random order from the entire 360 degree range—in contrast to procedures used to study spontaneous fluctuations (15–20), in which only one stimulus is presented. To reduce spontaneous fluctuations, stimuli were brief (0.5 s).

Each twofold ambiguity at a different stimulus orientation could have been resolved as an independent stochastic decision, which would have yielded an isotropic pattern of perceptual decisions across stimulus orientations. As we shall show, however, perceptions at different orientations are far from isotropic, following a pattern that is both highly stereotypical and idiosyncratic. The individual

Significance

Studies of perception usually measure overt variables—how sensory stimulation governs what is perceived. Here we show that perception is also governed by hidden variables that we call perceptual states. These hidden variables—two of which we study in this paper—can be inferred as systematic biases governing the perception of two families of ambiguous 3D stimuli. They vary widely across individuals, causing observers to often perceive the same stimulus in opposite ways. The variables change cumulatively over time and thus constitute a previously unknown type of perceptual memory. We document dynamics on time scales from minutes to months (the latter scale virtually unknown in perception), showing that aspects of the variables’ behavior can be modeled by random walks.

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Data deposition: The large datasets from the internet experiments (experiments 1 and 3) have been deposited at <https://osf.io/hk82s/>.

¹To whom correspondence should be addressed. Email: mark.wexler@parisdescartes.fr.

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generates such a time series has its own state—the information retained from past values. Predictive series have correlated values, power spectra that vary with frequency, and mean distance between samples that depends on lag. Moreover, predictive series can be either stationary—with properties such as mean and variance independent of time—or nonstationary. Stationary series fluctuate in an autocorrelated fashion about fixed values, whereas nonstationary series, such as random walks, can wander away. The finding in experiment 1 that the biases change more over 1 y than over 2 wk is a first indication that the bias time series retain state information.

To study bias time series in greater detail, we performed a second large-scale internet-based study in which we measured the SFM and TFM biases once a day for about 3 mo in a group of 97 participants, yielding an average of 87.8 nearly daily measurements for each. The daily measurements were performed similarly to experiment 1, each involving a block of randomly ordered, equally spaced 48 trials. Representative examples of the time series are shown in Fig. 3 and for all participants in *SI Appendix, Table T2*. There was an almost bewildering variety of individual behaviors: stability (Fig. 3*D*), slow drifts with constant speed (Fig. 3*E*) or variable speed (Fig. 3*A* and *F*), temporary excursions (Fig. 3*F*), abrupt transitions (Fig. 3*B*), oscillations between discrete values (Fig. 3*B* and *C*), and oscillations at multiple frequencies (Fig. 3*C*). Although we cannot exclude that perhaps some of the abrupt transitions were due to changing experimental conditions that were not under our complete control, the slow and regular drifts are very likely to represent authentic evolution in the state variables, all the more so when the drift occurred in one of the variables but not the other (as was often the case; *SI Appendix, Table T2*).

To quantitatively characterize the time series, we calculated several types of macroscopic statistics. First, we calculated the temporal power spectra of the bias vectors (Fig. 3*G* and *H*). Spectra for both SFM and TFM had peaks at low temporal frequencies that fell off and then flattened out at higher frequencies. Linearly regressing the individual participant's spectra on a log-log scale, we found that 95% of the SFM spectra and 98% of the TFM showed decreasing power with higher frequencies. Second, we calculated the mean squared Euclidean distance (MSED) between the measurements as a function of lag—days between measurements. We found that MSED increased with increasing lag (Fig. 3*I* and *J*); performing a linear regression of MSED versus lag, we found that 79% of the participants had biases that systematically drifted farther apart with increasing lag. (Many of the others had biases that wandered off only to loop back near their initial values.) Stationary series should have a mean distance that flattens out for large lag; the functions in Fig. 3*I* and *J* show no evidence for such flattening, at least for averaged data. Third, we calculated autocorrelations of the differenced time series and found a nonzero autocorrelation at lag 1 (see *SI Appendix, Fig. S7* for details). These observations strongly imply that biases are predictive, stateful time series and suggest that they are nonstationary.

To characterize the microscopic behavior of the time series, we modeled them within the Box-Jenkins autoregressive integrated moving-average (ARIMA) framework (35). Briefly (for details, see *SI Appendix*), we first searched a space of model families, including white noise, to find one that best approximated each series (the Cartesian components of each participant's SFM or TFM series were modeled separately). We found that only 18% of the SFM series and 24% of the TFM series were best fit by stateless, white-noise processes. One model family, integrated moving average or IMA(1, 1), was much more common than the rest. The autocorrelation functions of the differenced series (*SI Appendix, Fig. S7*) also strongly imply that the series were IMA(1, 1). In a second step, we fitted all of the individual series with models from this family and found that 93% of the SFM and 88% of the TFM series were well fitted, as revealed by a randomness test on the residuals.

The IMA(1, 1) family are series v_t with the following dynamical behavior: $v_t = v_{t-1} + \varepsilon_t - b\varepsilon_{t-1}$, where ε_t is an independent identically distributed (i.i.d.) variable. It can be shown (35) (also see *SI Appendix*) that such time series are equivalent to “random walks” or “Brownian motion” subject to measurement noise. In other words, an underlying state variable, u_t , was given by the random walk $u_t = u_{t-1} + \alpha_t$, where α_t , the random step, is an i.i.d. variable with variance σ_α^2 . This variable constitutes the system's memory, its cumulative value being carried over from one measurement to the next: Although successive steps are independent, their effects are cumulative. However, the state variable was not observed directly but filtered through independent measurement noise: $v_t = u_t + \beta_t$, where β_t , the measurement noise, is i.i.d. with variance σ_β^2 . We found that the median random step σ_α in our population was 0.022 [0.009, 0.041] (25/75 percentiles in brackets) for SFM and 0.020 [0.008, 0.036] for TFM, with our variables ranging from -1 to $+1$. The measurement noise σ_β was 0.103 [0.068, 0.144] for SFM and 0.122 [0.078, 0.157]. In terms of bias angles, the maximum median steps were 1.3 and 1.2 degrees for SFM and TFM and measurement noise 6.3 and 7.4 degrees. The power spectrum of a noisy random walk asymptotically approaches $1/f^2$ at low frequencies (the random walk component) and flattens out at high frequencies (the white noise), precisely what we found in the mean power spectra (Fig. 3*G* and *H*). The model predictions, shown in red in Fig. 3*G–I*, are at least good qualitative approximations to the macroscopic statistics of the time series.

Similar to the population distribution experiment, we found no trace of correlation between the daily values of the SFM and TFM biases. However, we did find moderate but robust correlations between the magnitudes of the daily steps in the SFM and TFM biases, both within and between participants (*SI Appendix*).

A histogram of all of the daily bias directions is shown in *SI Appendix, Fig. S8*. These distributions strongly resemble those obtained in experiment 1 (Fig. 2*C* and *F*), namely having peaks near the cardinal directions, with the same left-right and top-bottom asymmetries, on an almost completely different sample (10 out of 97 participants had participated in experiment 1). A simple random walk model obviously cannot account for all features of the data, such as the nonuniform bias distributions or the structured macroscopic features of the individual time series (Fig. 3). Even so, the random walk model gives a surprisingly good fit to intraindividual statistical properties of the time series (see Fig. 3, for instance).

Experiment 4: Short-Term Temporal Dynamics. To check if the biases had stateful behavior on time scales shorter than 90 days, we performed a laboratory experiment in which SFM bias was repeatedly measured over 90 min in 15 participants. We presented a sequence of stimuli lasting 30 min, resulting in a mean of 13 independent measures of the bias. To compare the roles of external stimulation and internal dynamics in driving bias change, we also measured the bias once 30 min before and once 30 min after this sequence, with the participants remaining in complete darkness in the intervening periods.

The individual bias time series are shown in *SI Appendix, Fig. S9*. Spectral power that decreases with frequency, increasing distance between biases with lag, and autocorrelations all point to stateful series that can be modeled as noisy random walks (*SI Appendix*). In three cases, the bias changed significantly after 30 min in complete darkness (marked by asterisks in *SI Appendix, Fig. S9*), suggesting that internal CNS dynamics can drive change in the bias variable. We found that biases changed faster during the 30-min sequences of continuous measures than over the 30 min of darkness (see *SI Appendix* for details). Thus, repeatedly showing SFM stimuli over many hundreds of trials seems to “excite” change in the bias variable. [Another finding of experiment 4, performed in complete darkness with nothing but the stimulus visible, is that the cardinal peaks in the bias direction distributions (Fig. 2*C*)—also found here—do not seem to be caused by visual edges with cardinally oriented orientations (monitor edges, etc.; see *SI Appendix* for details).]

Experiment 5: Deliberate Perturbation of State Variables. We wondered whether it is possible to modify the values of the state variables using visual stimuli. We measured observers' SFM and TFM biases and then perturbed them for about 30 s using stimuli whose depth was unambiguously specified by the addition of binocular disparity and whose tilts or motion directions differed from the biases by 90–135 degrees, alternating the direction of the perturbation on successive blocks. Following this sequence of perturbing stimuli, we remeasured biases over a 100-s period, using a multiblock design to increase the temporal resolution of the measurement down to 1–2 s (*SI Appendix, Fig. S10*).

Results for individual participants (see Fig. 4 for a representative participant and *SI Appendix, Fig. S11* for all participants) show that the aftereffect of the perturbation on the bias variable was attractive, “pulling” the bias variable toward the perturbation, but with decay toward the preperturbation value over several tens of seconds. Fitting exponential decay functions to the time evolution curves, we found that the amplitude of the effect immediately following the perturbation had a median value of 37.2 degrees in SFM and 41.7 degrees in TFM, with effects significantly attractive in all participants and conditions. The half-life of the perturbation—the time it takes for the effect to decay to half its initial value—had median values of 21.1 s for SFM and 42.4 s for TFM.

Experiment 6: Effect of Bistable Fluctuations on Biases. Any one of our ambiguous stimuli, when repeatedly presented at the same orientation, is bistable: Its perception spontaneously fluctuates between the possible interpretations (15–20). We wondered whether such fluctuations modify the state variables, temporarily or durably. We first measured SFM bias direction in six participants. Then, we repeatedly exposed each participant to the surface oriented at his or her own bias tilt, until obtaining a spontaneous tilt reversal that persisted for 10–20 stimulus presentations (several tens of seconds), so that the participant perceived the tilt opposite to his or her own initial bias. We then remeasured the bias in the usual way over the next several minutes. We found (*SI Appendix, Fig. S12*) that the bias returned to near its original value in all participants in at most a few minutes. Thus, fluctuations in bistable stimuli seem to have, at most, short-term effects on the state variables.

Experiment 7: Existence of the Bias Before the First Stimulus. Studies of bistable perception have brought to light a phenomenon known as sensory or perceptual memory, where a single interpretation of

an intermittently presented stimulus can last for a large number of trials (17, 19, 20). Are state variables sensory memories formed at or near the first stimulus, or do they exist in the visual system before exposure to our stimuli? To answer this question, we performed an experiment using SFM stimuli on 30 participants, with responses recorded from the very first stimulus (i.e., no practice trials). We predicted that if the biases were sensory memories, then the response on the first trial would be completely random and unbiased but then become “frozen in” as a sensory memory, in effect becoming the bias. A more complex version of the hypothesis would have the vector average of the responses on the first n trials becoming the sensory memory. For each i , we calculated the absolute angular difference between the bias direction calculated using trials 1, $\dots$, i and the bias direction from all trials. The sensory memory hypotheses predicted local minima in this curve. We found no evidence for such local minima, and the data were in perfect agreement with a simple model of preexisting bias (see *SI Appendix, Fig. S13* for details). Thus, experiments 6 and 7 both show that the state variables are independent of bistability phenomena, namely of spontaneous reversals and sensory memory.

Discussion

Although most studies of perception emphasize processes that are largely universal across measurements on different observers and different points in time, we have demonstrated large-scale differences among observers that undergo stateful, cumulative fluctuations over time scales from tens of seconds to months. There have been several recent reports of stable idiosyncratic biases arising in different contexts in human vision (36–40). Here, we have shown for the first time, to our knowledge, that two of these biases are state variables, in two different ways. First, we found that the appearance of suprathreshold stimuli depends not only on the stimulus but also strongly on the bias variables' values. Second, the variables retain information about their past values when undergoing fluctuations in time, with their temporal dynamics at least partly described by a random walk model. Although the successive steps in the random walk are independent, its value accumulates the steps and constitutes a new kind of perceptual memory. Although random walk or diffusion models have been used to account for neurophysiological and behavioral data on perceptual decision making and other processes on brief time scales (41, 42), perceptual parameters have not previously been shown directly to undergo random walks, and on time scales as long as several months.

An open question is what drives change in the state variables: visual stimuli (if so, which ones) or internal dynamics. Our results suggest that both factors can drive change: On one hand, state change can be primarily stimulus-driven (cf. the perturbation experiment); on the other hand, state change seems to sometimes occur in total absence of external visual stimulation (the short-term temporal dynamics experiment). Results showing the importance of endogenous (43) and initial (44) perceptual decisions to subsequent cue learning may be germane to these issues.

The continuous presentation of an unchanging ambiguous stimulus (e.g., an SFM or TFM stimulus at a fixed orientation) leads to spontaneous fluctuations between the two interpretations usually every several seconds (15, 16, 18), whereas intermittent presentation leads to a lengthening of the duration of each interpretation up to several minutes, a phenomenon known as sensory memory (17, 19, 20). The main methodological difference between studies of these bistability phenomena and our studies is that we present successive stimuli at different orientations rather than repeating the exact same stimulus. The spontaneous fluctuations found in the bistability studies also exhibit a kind of perceptual state or memory, because successive interpretations are correlated. In experiments 6 and 7, however, we have shown that spontaneous fluctuations do not lead to long-term changes of the state variables and that the state variables are unlikely to be sensory memories newly formed by exposure to our stimuli. However, state variables may be closely related to the independent and idiosyncratic initial phase of bistable fluctuations, known as onset rivalry (36, 45).

Fig. 4. The effect of deliberate perturbation on the biases using nonambiguous stimuli (experiment 5). Data are shown for one representative participant for TFM stimuli (data for all participants are shown in *SI Appendix, Fig. S11*). The x axis shows the time immediately following the perturbation in seconds. The y axis shows the effect of the perturbation: the difference in degrees between the measured direction bias and the initial, preperturbation bias. On every other block, the perturbation stimuli were chosen between +90 and +135 degrees away from the initial bias direction (blue dots, bars, and curves), whereas on the other blocks the perturbation was in the opposite direction, between −90 and −135 (orange). Error bars denote SEs over multiple blocks. The curves are exponential fits.

We have demonstrated the existence of two state variables that have the same formal structure and whose instantaneous values are independent (the amplitudes of their changes are weakly but robustly correlated). This raises the question of the universality of this perceptual structure. Recently, the perception of a third family of stimuli—ambiguous one-dimensional apparent motion—has been shown to admit the same kind of biases as studied here (40). Semicircular-shaped biases with individual differences are not limited to vision: An identical structure is found in hearing (46). It is not known whether these other biases show stateful behavior, what their temporal dynamics may be like, and whether they have any correlations with the two variables studied here. It would be interesting to know how many other state variables might there be and if some variables control more than one type of stimulus.

The presence of state in perceptual processes pleads in favor of recurrent neural architectures, which represent state in a natural way (25, 26). Brain imaging studies of the related phenomenon of bistable perception have identified activity in ventro-occipital and intraparietal as well as frontoparietal regions (47–49) correlated to transitions between states. Interestingly, some of the interindividual variability in perceptual dynamics of bistable perception is correlated with local gray-matter density in the parietal cortex (50). It would be interesting to check whether these functional activations or anatomical features are correlated parametrically to the values of the state variables or to their transitions. Another line of research for future studies will be to determine the genetic contributions to individual variations in our state variables,

similarly to what has been done for bistable perception (51). If the state variables capture at least some functional aspects of the underlying neural networks, the identification and measurement of these variables may open the door to a psychophysics of neural state.

Methods

Trials typically consisted of twofold ambiguous SFM or TFM stimuli presented at different orientations in random order for 500 ms, after which the participant chose one of the two shape (SFM) or motion (TFM) percepts compatible with the stimulus. Experiments 1 and 3 were performed by participants on their own computers and ran inside internet browsers and were implemented in Javascript and HTML5. Experiments 2 and 4–7 were performed in the laboratory using more traditional methods. For further details, see *SI Appendix*. Informed consent was obtained prior to all experiments in accordance with the Declaration of Helsinki. In France, the legal ethics committees do not examine non-invasive behavioral studies.

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