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Report

Predictive Properties of Visual Adaptation

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Summary

What humans perceive depends in part on what they have previously experienced [1, 2]. After repeated exposure to one stimulus, adaptation takes place in the form of a negative correlation between the current percept and the last displayed stimuli [3–10]. Previous work has shown that this negative dependence can extend to a few minutes in the past [5, 11, 12], but the precise extent and nature of the dependence in vision is still unknown. In two experiments based on orientation judgments, we reveal a positive dependence of a visual percept with stimuli presented remotely in the past, unexpectedly and in contrast to what is known for the recent past. Previous theories of adaptation have postulated that the visual system attempts to calibrate itself relative to an ideal norm [13, 14] or to the recent past [5, 7, 10, 15, 16]. We propose instead that the remote past is used to estimate the world's statistics and that this estimate becomes the reference. According to this new framework, adaptation is predictive: the most likely forthcoming percept is the one that helps the statistics of the most recent percepts match that of the remote past.

Results

In a first experiment, human observers participated in a binocular rivalry study where their percept can match either the stimulus presented to their left or right eye [17–19]. Stimuli in rivalry between the two eyes were Gabors that differed in orientation (left and right) and spatial frequency (the number of stripes). They were preceded by nonrivalrous series of one to four Gabors (either left or right oriented) displayed sequentially (Figure 1B). Spatial frequency was different between the nonrivalrous Gabors of the series and the rivalrous Gabors: spatial frequency during rivalry was higher in one eye and lower in the other (Figure 1A). We asked observers to report their first perceived spatial frequency in binocular rivalry (higher or lower) after each series of nonrivalrous Gabors. Perceived orientation was then deduced from the reported perceived spatial frequency. We deliberately asked observers to report spatial frequency rather than orientation in order to draw their attention away from the variable that was manipulated. We then systematically analyzed the dependence of the rivalry percepts to events presented within windows of varying durations and at different times in the past.

Correlation between Displayed Stimuli and Current Percept

We first looked at perceived orientation in the rivalrous stimulus as a function of displayed orientations in a window including only the last series (window size = 1 and window position = 1, Figure 1C). Then we extended the window to include more series other than the one adjacent to the current response (window size > 1 and window position = 1). An original aspect of the present analysis is that we also introduced a gap between the current response and the window (window position > 1, Figure 1D) thereby allowing us to study the influence of remote history independently of the recent one.

Figure 2A shows the correlation between the perceived left orientation and the proportion of displayed left orientations in a given window of past series. In the analysis we varied the window size and position (in time) relative to the current response. Windows with significant correlations are surrounded by black outlines, after control for type I errors (see Experimental Procedures). These significant windows belong primarily to two subspaces. The first subspace includes windows adjacent to the current response or near the current response (positions < 7): the displayed orientation within these windows is negatively correlated with the current percept. The second subspace includes windows further away from the current response, and these are positively correlated with the current percept.

We will refer to the windows in the first subspace as the "recent history." The more the left-oriented Gabor is presented in the recent history, the less the left orientation is perceived in binocular rivalry. This relationship is characteristic of adaptation: after exposure to a stimulus, this stimulus becomes less likely to be perceived again [10, 20]. We then refer to a window in the second subspace as the "reference" and call it *H*. The more the left orientation is displayed in the reference, the more the left orientation is perceived in binocular rivalry. This positive relationship between perceived orientation and displayed orientation clearly demonstrates that remote history influences perception of orientation in binocular rivalry.

Tilt After-Effect

In a second experiment, we replicated our results in a tilt after-effect paradigm. Observers now saw a series of Gabors that could have one of two orientations A and B. These orientations were separated by 40 degrees and were randomly selected for each participant (avoiding cardinal orientations). A test Gabor patch was subsequently presented and observers had to judge whether its orientation was closer to A or B. Unbeknownst to the observer, the orientation of the test was always exactly in-between A and B. As predicted from our results on binocular rivalry, the history of the A and B series significantly influenced the perceived orientation of the test Gabor. Perceived orientation was biased away from the displayed orientations within a recent window of stimuli and toward the displayed orientations within a reference window of stimuli further in the past (Figure 2B).

Model of Predictive Adaptation

We propose that both relationships (negative in recent history and positive in the reference) can be explained by a single mechanism: predictive adaptation. Predictions are made for the next event according to the simple rule that the distribution

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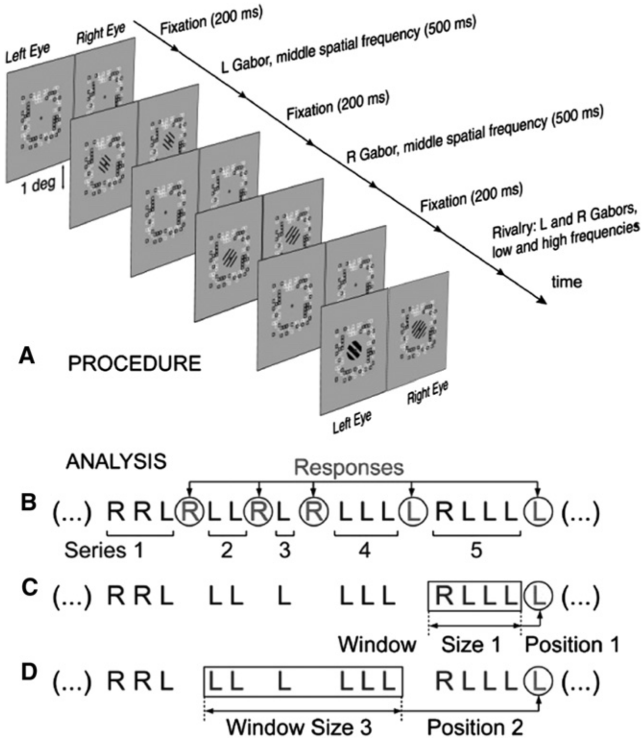

Figure 1. Procedure and Analysis

(A) Procedure: observers saw a series of randomly left (L)- and right (R)-oriented Gabors identical in both eyes followed by two Gabors that were in rivalry (different orientations and spatial frequencies between eyes). The series LR is given here as an example.

(B) The analysis tries to explain the perceptual responses for the rivalrous stimuli from the orientations displayed in the preceding series.

(C) The displayed orientations taken into account define a window. A window of size 1 and position 1 corresponds to the series adjacent to the current response.

(D) Windows with bigger sizes and at positions more remote in the past were tested. See also Figure S1.

of events in recent history should match the one observed in the reference. If a given proportion of visual objects A rather than B is observed in the reference, then the same proportion is expected in the recent history. If the proportion of objects A in the recent history is lower than the one in the reference, then an object A is expected as the next percept. Increasing the proportion of objects A in the recent history makes the object A less expected (and perceived). Increasing the proportion of objects A in the reference makes the object A more expected (and perceived). Interestingly, in making predictions this way, the visual system employs a similar strategy as the human reasoning system does in the case of the gambler's fallacy [21], exemplifying a local representativeness bias.

We designed a simple quantitative model to depict the essence of predictive adaptation that we illustrate for the results of the binocular rivalry experiment. First, to account for trivial idiosyncratic preferences, we denote by $\widehat{p}_H(L)$ the estimated probability of left orientation for any given reference H and relate it to the actual probability $p_H(L)$ by Bayes' rule:

$$\widehat{p}_H(L) = \frac{p_H(L) \cdot q_L}{p_H(L) \cdot q_L + (1 - p_H(L))(1 - q_L)}, \qquad (1)$$

where q_L is the prior for left orientation. Second, let m be the number of left-oriented Gabors displayed in the n Gabors of the recent history. Gabor $n+1$ is the current Gabor in binocular rivalry. Let r_L be the probability of observing the series completed by a $(m+1)^{th}$ left-oriented Gabor according to a binomial distribution with parameters $(n+1)$ and $\widehat{p}_H(L)$, the estimated probability of left-oriented Gabors in the reference. Similarly, r_R is the probability of completing the series with a right-oriented Gabor instead of a left-oriented Gabor. Predicted proportion of perceived left orientation for the current response t is thus

$$p_t(L) = \frac{r_L}{r_L + r_R}, \qquad (2)$$

where

$$r_L = \binom{n+1}{m+1} \widehat{p}_H(L)^{m+1} \left(1 - \widehat{p}_H(L)\right)^{n-m} \qquad (3)$$

and

$$r_R = \binom{n+1}{m} \widehat{p}_H(L)^{m} \left(1 - \widehat{p}_H(L)\right)^{n-m+1}. \qquad (4)$$

Model predictions are shown when the prior for left orientation was balanced, that is when q_L is 0.5 (Figure 3A).

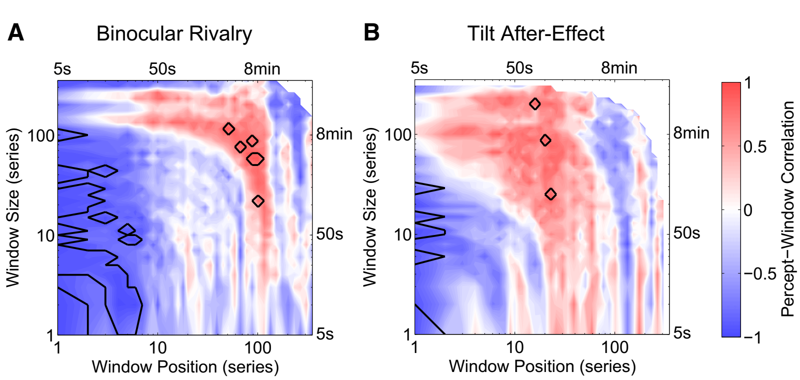

Figure 2. Results

(A) Binocular rivalry results. For windows of series varying in position and size, the correlation between proportion of displayed left orientations in that window and perceived left orientation is shown in blue when negative and in red when positive. Proportion of perceived left orientations is split in nine bins, all observers together. Black outlines indicate significant correlations after a Bonferroni correction (see Experimental Procedures). Windows of series adjacent to or very near the current trial present a strong and negative correlation with the current percept ($|r| \geq 0.85$). In contrast, windows further away and about 100 series long present a strong and positive correlation with the current percept ($r \geq 0.86$).

(B) Tilt after-effect results. Using the same format as in (A), different hues represent the correlation between the proportion of displayed "A" rather than "B" orientations in a window of varying position and size and the probability of seeing "A" in a test stimulus that is physically in-between "A" and "B." Windows of series adjacent to the current trial present a strong and negative correlation with the current percept ($|r| \geq 0.84$). In contrast, windows further away and about 100 series long present a strong and positive correlation with the current percept ($r \geq 0.89$). See also Figure S2.

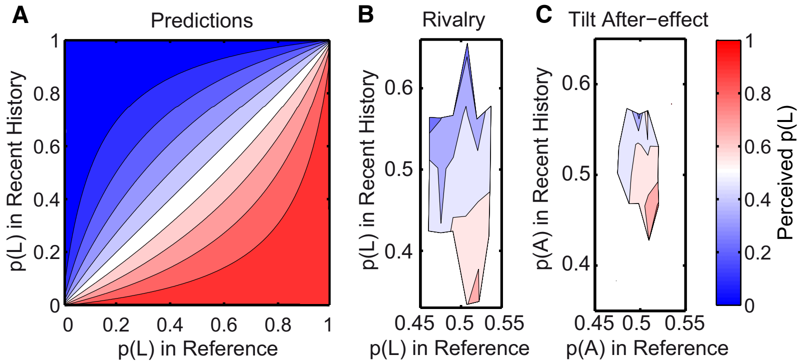

Figure 3. Relationship between Recent History and Reference

(A) Model predictions. According to the model, the proportion of perceived orientation left (rather than right) depends both on the proportion of left orientations displayed in the reference (abscissa) and left orientations in the recent history (ordinate). For this plot, the model's prior probability to see either left or right was set to 0.5.
(B) Binocular rivalry results. The plot shows the relationship in the binocular rivalry data between perceived "left" orientation in the test Gabor and the proportion of "left" orientations in the reference and recent windows.
(C) Tilt after-effect results. The plot shows the relationship in the adaptation data between perceived "A" (counterclockwise relative to standard orientation) orientation in the test Gabor and the proportion of "A" orientations in the reference and recent windows.

The model is able to capture the negative relationship between the perceived orientation in rivalry and the displayed orientations in the recent history (Figure 4A), as well as the positive relationship in the reference (Figure 4B). Similar results were obtained for the after-effect experiment (see Figure S3 available online). Results in the format of Figure 3A are displayed for comparison in Figures 3B and 3C.

We have interpreted our results as evidence for a mechanism predicting the next event from the proportion of past orientation events. In addition, the visual system might build a prediction from the alternation of events rather than the events themselves. No evidence was found in favor of that scenario (see Figure S2).

Discussion

Even though sensory adaptation is a well-established phenomenon, its origins are still debated. It is now clear that the once popular theory of neural fatigue is not able to account for adaptation [10]. Contemporary theories include error correction, decorrelation, and recalibration. Error correction allows the channels representing neurons sensitive to particular orientations to stay tuned even when the channels are not functioning properly [13, 14]. Error correction can be instantiated by measuring the distribution of recent activity across the channels and by correcting any discrepancy relative to a fixed distribution. Decorrelation refers to the modification of channels' sensitivity so that their activities remain uncorrelated [16, 22, 23]. Recalibration (or Gibson's normalization) involves the modification of the zero point [5, 7, 10, 15, 16], for instance via gain control [24, 25], on the perceptual continuum described by antagonist channels [16, 26]. The zero is usually set to the average recent activity.

In error correction, the central nervous system corrects the activity in the sensory channels by comparing it to a fixed distribution. The system is then forced to postulate a fixed (e.g., close to uniform) of each orientation in the world: the internal fixed distribution hypothesis can only be made during a critical period or during evolution and thus is not a learned hypothesis [13]. Our results are inconsistent with this hypothesis but suggest instead that the remote history (the reference) is treated as the world's true distribution. In contrast to error correction, decorrelation and recalibration do not postulate a fixed distribution and can deal with stimuli whose distribution is changing. However, decorrelation and recalibration only use the recent history of the perceptual attribute, which is typically defined by the adaptation duration needed to reach a maximum in the subsequent after-effect [5, 12]. Although adaptation processes are supposed to measure the recent distribution of the attribute during the adaptation period, they do not try to compare this distribution with the distribution that was observed before adaptation, similarly to what we found in the present experiment. Norm theory is an extension of the recalibration theory [7]. Although norm theory postulates that a long-term rather than a short-term history is measured, it is still inconsistent with our results because we found that remote stimuli were positively correlated with the current percept, not negatively. Furthermore, norm theory does not try to compare the long-term distribution with an older history or a more recent one. Without these two measures, it cannot account simultaneously for the positive and negative relationships we found. Other recent attempts to model adaptation,

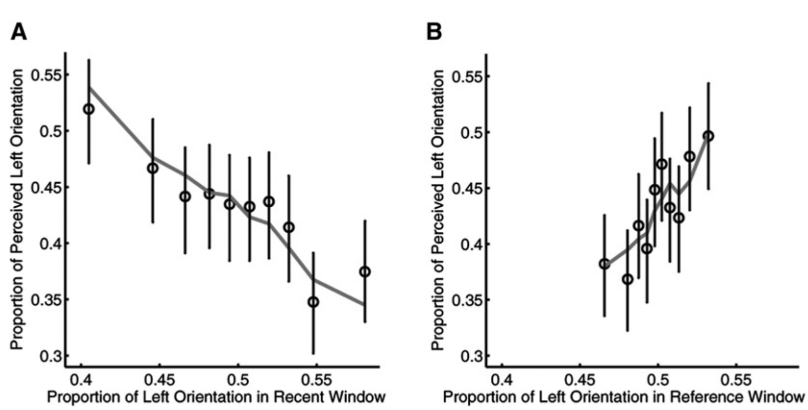

Figure 4. Model Results

For each observer of the binocular rivalry experiment, a prediction was made for each possible trial for a reference window of size 101 at position 58 and recent history at position 1 (as inferred from the results shown in Figure 2). The model was run using the recent history size as free parameter (best parameters are in Table S1, average recent size = 35). The average proportion of the displayed left orientations in the reference window was used to estimate the bias q_L. Predictions (solid lines) and data (open black circles) for the percentage of left orientations as a function of left orientations in the recent history (A) or in the reference (B) are presented averaged across observers after being grouped in ten bins. Error bars are bootstrapped 95% confidence intervals. The same analysis for the tilt after-effect experiment can be found in Figure S3 and Table S1.

including those within the Bayesian framework [27], are also inappropriate because they can only account for the negative correlation that we found with the recent history. Finally, we should note that in the correlation analysis, we found a long-term negative dependence (Figures 2A and 2B) that did not survive significance tests in subsequent analyses. This type of long-term negative dependence may reflect some long-term adaptation recently found in color [28, 29], orientation [30], and faces [6].

In conclusion, in two experiments on orientation judgments, we found both a negative correlation of the current percept with visual events presented just before and a positive correlation with a remote reference window of stimuli. We propose a model of predictive adaptation according to which the visual system uses the reference as an estimate of the world's statistics that is then combined with recent history for predicting the next percept. Implicit predictions are based on the assumption that the distributions of orientations should match between recent history and the remote reference. The recent history is composed of the last hundred visual events on average (3 min). The reference is a window of around 300 visual events long (8 min), not adjacent to the current response but beginning between 70 events in the past for the adaptation experiment (from 2 to 10 min in the past) and 200 events for the rivalry experiment (from 5 to 13 min in the past). The next challenge will be to understand how the visual system neurally implements predictions over such a long stream of events.

Experimental Procedures

Stimulus and Material

In the binocular rivalry experiment, stimuli were 500 ms Gabor patches preceded by a 200 ms blue fixation dot. Gabors were sinusoidal variations of luminance (mean: 15 cd.m^{-2}) embedded in a Gaussian envelope (0.25° at half height). They were left or right oriented (respectively rotated 45° counterclockwise and 45° clockwise from vertical) and covered a circular area of 1°. Gabors were displayed between one and four times (thereby defining a series, whose average size was three). Each series that was used (see Figure S1) was presented 32 times. Immediately afterwards, a 200 ms red fixation dot was followed by two Gabors in rivalry (orthogonal orientations across eyes, Figure 1A). The rivalrous Gabor's spatial frequency was 2.5 cycles.deg^{-1} (cpd) in one eye and 4.5 cpd in the other eye. The spatial frequency of the Gabors in the series was 3.5 cpd. Vergence was maintained by a group of small squares surrounding the stimuli. Binocular rivalry was achieved by using a modified Wheatstone stereoscope with a chin rest.

In the tilt after-effect experiment, stimuli were identical with the following exceptions. Gabors in the series were oriented either 20° to the left or to the right of the test Gabor. The test Gabor orientation was randomly selected for each participant in the following set [40°, 50°, −40°, −50°] (where zero is vertical). All the possible series (with maximum size four) were used with the exclusion of constant ones (e.g., "A-A-A"). Consequently, no series of size 1 was used. Gabor spatial frequency was kept constant at 3.5 cpd, including the test Gabor.

Stimuli were generated with the PsychToolBox library [31, 32] on an Apple Mac G4. They were displayed on a 21 in CRT monitor at a frame rate of 60 Hz and a resolution of 1,650 × 1,050 pixels.

Observers

Eight observers for the rivalry experiment and nine observers for the after-effect experiment with normal or corrected vision participated in the experiment (one participated in both experiments). Two additional participants were excluded from rivalry experiment because they had a strong preference for perceiving one orientation in rivalry (>80% of the responses).

Procedure

In the binocular rivalry experiment, the contrast ratio between eyes was first calibrated to achieve a 0.5 probability of perceiving the left eye image. Then, the participants' task was to decide whether the spatial frequency of the perceived rivalrous Gabor was lower or higher than the spatial frequency of the nonrivalrous Gabors presented during the series. The rivalrous Gabors were displayed until observers indicated their response. Rivalrous spatial frequencies were counterbalanced between eyes and orientations. In the tilt after-effect experiment, Gabors with orientations A and B were displayed followed by a 200 ms test Gabor, whose orientation was in-between A and B. Participants' task was to decide whether the test Gabor was oriented more like the orientation A (counterclockwise) or B (clockwise).

Correlation Analysis

Responses as a function of the proportion of left-oriented Gabor in the window are pooled across observers for a window of a given size and position. The pool is split into nine bins of increasing proportion of left-oriented Gabors. Pearson correlation is computed between the proportion of perceived left-oriented Gabor and left-oriented Gabor displayed in the window. This correlation is bootstrapped (5,000 repetitions) to get a confidence interval at a threshold p corrected by Bonferroni ($p = 3.75 \times 10^{-5}$). The Bonferroni method avoids the inflation of the familywise error rate. Significant correlations do not include the zero in their confidence interval.

Supplemental Information

Supplemental Information includes three figures and one table and can be found with this article online at doi:10.1016/j.cub.2012.02.021.

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