

Chronic and acute biases in perceptual stabilization

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When perceptually ambiguous stimuli are presented intermittently, the percept on one presentation tends to be the same as that on the previous presentation. The role of short-term, acute biases in the production of this perceptual stability is relatively well understood. In addition, however, long-lasting, chronic bias may also contribute to stability. In this paper we develop indices for both biases and for stability, and show that stability can be expressed as a sum of contributions from the two types of bias. We then apply this analytical procedure to binocular rivalry, showing that adjustment of the monocular contrasts can alter the relative contributions of the two biases. Stability is mainly determined by chronic bias when the contrasts are equal, but acute bias dominates stability when right-eye contrast is set lower than left-eye contrast. Finally, we show that the right-eye bias persists in continuous binocular rivalry. Our findings reveal a previously unappreciated contribution of chronic bias to stable perception.

Introduction

What we see depends not only on what we look at, but also on preexisting biases and expectations. Ordinarily, the operation of such factors may go unnoticed but their influence can be made patently

obvious when the visual stimulus is ambiguous or conflicting. Under those conditions, visual perception tends to become unstable: what we perceive fluctuates over time between alternative visual interpretations, even though what we are looking at remains invariant. Textbook examples of visual instability include binocular rivalry (Alais & Blake, 2005), motion-induced blindness (Bonneh, Cooperman, & Sagi, 2001), ambiguous figures (Long & Toppino, 2004), ambiguous apparent two-dimensional motion (Terminus, 1938) and ambiguous three-dimensional rotational motion (Miles, 1931). One of the interesting properties of multistable perception, as this phenomenon is called, is the tendency for fluctuations in perception to transpire unpredictably over time, without any willful intent on the part of the subject (Brascamp, van Ee, Pestman, & van den Berg, 2005). It is as if the brain attempts to infer what one is seeing but fails to arrive at a stable, unequivocal answer (Leopold & Logothetis, 1999; Sterzer, Kleinschmidt, & Rees, 2009).

Those different instances of bistable perception, while fascinating in their own right, take on additional interest because of their propensity to exhibit two forms of dependence on what may be called biases or expectations. First, a given subject may exhibit a long-term, intrinsic bias for a given perceptual state. This

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kind of bias can be defined as a reliable, enduring departure from equal likelihood of alternative percepts; we refer to this here as chronic bias. One example of chronic bias is the tendency for a subject to favor perceptual dominance of whatever stimulus is being viewed by a given eye during binocular rivalry. In several large data sets, investigators have found a tendency for one eye to dominate during rivalry for a given subject, with the preferred eye varying among subjects (Ehrenstein, Arnold-Schulz-Gahmen, & Janschinski, 2005; Ooi & He, 2001; Porac & Coren, 1976; Yang, Blake, & McDonald, 2010). Subject-specific chronic biases have been found in binocular rivalry (Carter & Cavanagh, 2007; Pearson & Clifford, 2004; Stanley, Carter, & Forte, 2011) and for other ambiguous stimuli, such as structure-from-motion (de Jong, Knapen, & van Ee, 2012; Knapen, Brascamp, Adams, & Graf, 2009) and the Necker cube (Sundaeswara & Schrater, 2008).

A second factor that is of influence during multistable perception, is a relatively short-term dependence on prior perception. It can be defined as a positive pairwise correlation between perceptual dominance over two successive, discrete exposures to ambiguous or conflicting stimulation (Leopold, Wilke, Maier, & Logothetis, 2002; Orbach, Ehrlich, & Heath, 1963; Pearson & Brascamp, 2008). Perceptual dominance, in other words, tends to persist across periods when the provoking stimulus is physically removed. In this paper, we refer to this form of perceptual memory as acute bias.

The neural mechanisms underlying chronic and acute bias are presently unclear, but it seems likely that the two types of bias have distinct neural origins. Chronic bias appears to be a learned response to repeated visual exposure. For example, Porac and Coren (1976) provide evidence that sighting dominance is probably the most significant type of ocular dominance and surmise that it is “useful to have the dominant eye aligned with the dominant hand, such as in aiming a pointer” (p. 888). Again, Sundaeswara and Schrater (2008) found that there is a bias toward seeing the Necker cube from above, the view that is presumably more frequent in natural scenes. Mechanisms underlying acute bias, in contrast, might include transient changes in membrane potential or synaptic efficacy, as has been suggested in modelling work (Noest, van Ee, Nijs, & van Wezel, 2007; Wilson, 2007).

Although it is generally agreed that both chronic bias and acute bias play a role in determining perception of multistable stimuli, the two are not easy to separate. For instance, if a series of presentations of a given stimulus yield the same percept, is it because of sequential dependence acting between consecutive presentations, or is it because of a chronic bias existing

before the first stimulus appeared? In this study, our goal was to develop a principled, quantitative strategy for distinguishing chronic from acute bias. This strategy goes beyond approaches that focus primarily on the probability of percept repetition during repeated presentation of a multistable stimulus by providing explicit operational definitions of chronic bias and acute bias.

Methods

Subjects

Two subject cohorts, standard and large, were studied. The standard cohort comprised 21 subjects who were each studied over a number of experimental sessions. They were recruited from staff and students at the University of Sydney (14 female, seven male), and their ages ranged from 22 to 55 years. Not all subjects were available for all experiments. The 50 subjects in the large cohort (29 female, 21 male; aged 18–47 years) were each studied for one hour with the aim of improving the statistical reliability of several key measures. Subjects in the large cohort were recruited mainly from the University’s undergraduate population. All subjects from both cohorts, apart from author MA, were paid for their time and were unaware of the aims or results of the experimental work. The clinical requirements for inclusion in the study were a visual acuity of 6/6 or better in each eye and a stereoptic threshold of 1 min or better, where the latter was measured with the Titmus test.

Apparatus

Visual stimuli were presented on a cathode ray tube monitor (Philips 105S; Philips International B. V., Amsterdam, The Netherlands) with a spatial resolution of 60 pixels/° and a temporal resolution of 72 frames/s. Chromaticity (CIE 1931 2°) was gray ($x = 0.296$, $y = 0.328$) and background luminance was 41 cd/m². Subjects used a stereoscope with front-surfaced mirrors to view the monitor. Stimuli for the left and right eyes were presented on the left and right sides, respectively, of the monitor. Subjects used the stereoscope’s chinrest and forehead rest to stabilize their view, and the optical distance from eye to monitor was 1.14 m. Stimulus chromaticity was measured independently through each stereoscope eyepiece. Luminance differed between eyes by less than 3%, and measured contrast matched contrast setting to within 3% for each eye. Experiments were

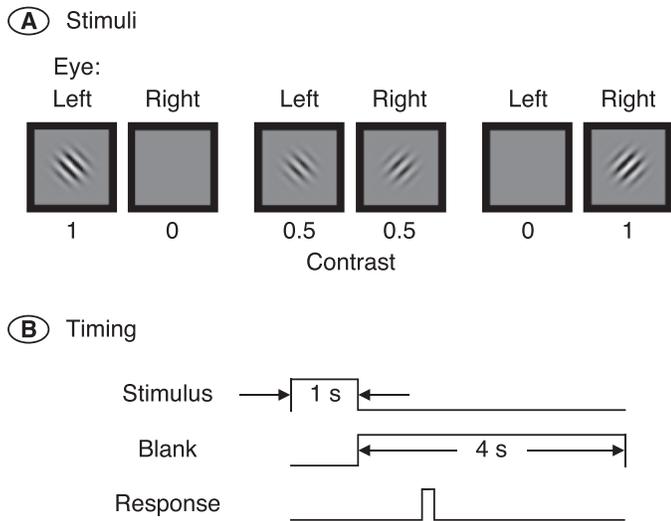


Figure 1. Stimulus spatial form and timing. (A) The stimulus was a Gabor patch tilted 45° from the vertical for one eye and an orthogonal patch for the other eye. The monocular contrasts could differ, as shown by the three examples, but their sum was always 1. (B) On each trial the stimulus was delivered for 1 s and then removed for 4 s. The subject used the blank period to signal the percept produced by the stimulus.

conducted in a darkened room so that the only light visible to the subject was from the monitor.

Stimulus

The central pair of images in Figure 1A illustrates the stimuli used throughout this study. A Gabor 45° from vertical was presented to one eye and an orthogonal Gabor was presented to the fellow eye. Each Gabor was calculated by multiplying two functions, a cosine with a spatial frequency of 3 cycles/° and a Gaussian envelope with a standard deviation of 0.3°. Luminance was maximal at the center of the Gabor. Contrast was calculated by subtracting background luminance from this maximum, and dividing the difference by background luminance. The contrast of the left- and right-eye stimuli always summed to 1: three examples of the stimuli used are shown. Each Gabor was surrounded by a thick black border to aid binocular fusion. The square enclosed by the border was 2.5° wide and the border width was 0.25°.

Analysis

This analysis defines three perceptual quantities—stability, acute bias, and chronic bias—and derives the relationship between the three.

Percept on second trial

	1	2	Sum
Percept on first trial			
1	p_{11}	p_{12}	p_1
2	p_{21}	p_{22}	p_2
Sum	p_1	p_2	1

Table 1. Definitions and sums of percept probabilities.

Definitions

Assume that each trial in an experiment results in one of two possible percepts, 1 or 2. For two successive trials we define the probability of the percept pair p_{ij} as shown in Table 1. The table also shows the probability of a percept, p_i , on a single trial. This is given by the row sum because, for example, percept 1 must be followed by percept 1 or 2:

$$p_1 = p_{11} + p_{12}, p_2 = p_{21} + p_{22} \tag{1}$$

The probabilities p_i are also given by the column sums because any percept must be preceded by one or the other percept:

$$p_1 = p_{11} + p_{21}, p_2 = p_{12} + p_{22} \tag{2}$$

The four probabilities are not independent because their sum defines the certain event,

$$p_{11} + p_{12} + p_{21} + p_{22} = 1 \tag{3}$$

and, in an infinite sequence of trials, each transition from percept 1 to percept 2 is eventually followed by the opposite transition,

$$p_{12} = p_{21} \tag{4}$$

Thus, there are only two independent probabilities.

We now define three perceptual indices: stability, acute bias, and chronic bias. Each index is defined so that its value is zero in the absence of the effect it quantifies. Stability measures the probability that the percept remains the same from one trial to the next,

$$\text{stability, } s = p_{11} + p_{22} - (p_{12} + p_{21}) \tag{5}$$

This index is zero if the probability that consecutive percepts are the same equals the probability that they differ, as required. The second index, acute bias, is the component of stability for which one percept depends on the previous one. It is calculated by subtracting from the probability of a percept pair, p_{ij} , the probability expected if the two percepts are independent: $p_{ij} = p_i p_j$. Thus

$$\begin{aligned} \text{acute bias, } a &= s - (p_1 p_1 + p_2 p_2 - p_1 p_2 - p_2 p_1) \\ &= p_{11} - p_1^2 + p_{22} - p_2^2 \\ &\quad - (p_{12} - p_1 p_2 + p_{21} - p_1 p_2) \end{aligned} \tag{6}$$

Index	Limit	Percept sequence	p_2	p_{22}	Index value
s	Minimum	... 1212 ...	0.5	0	-1
	Maximum	... 1111 ...	0	0	1
		... 2222 ...	1	1	1
a	Minimum	... 1212 ...	0.5	0	-1
	Maximum	... 1111 ... 2222 ... , asymptote as single-percept sequence becomes infinite	0.5	0.5	1
c	Minimum	... 1111 ...	0	0	-1
	Maximum	... 2222 ...	1	1	1

Table 2. Minima and maxima of the perceptual indices.

Appropriately, this index is zero when successive percepts are independent. Third, chronic bias gives the probability that one percept occurs more often than the other,

$$\text{chronic bias, } c = p_2 - p_1 \tag{7}$$

Simplifying the indices

Given that there are only two independent probabilities p_{ij} , we can express stability in terms of acute bias and chronic bias. First, the indices are expressed in terms of p_{22} and p_2 , using Equations 1 to 4.

$$\begin{aligned} s &= 1 - (p_{12} + p_{21}) - (p_{12} + p_{21}) \\ &= 1 - 4p_{12} \\ &= 1 - 4(p_2 - p_{22}) \end{aligned} \tag{8}$$

To simplify acute bias, we first transform its first two terms,

$$\begin{aligned} p_{11} - p_1^2 &= 1 - (2p_{12} + p_{22}) - (1 - p_2)^2 \\ &= 1 - (2(p_2 - p_{22}) + p_{22}) - (1 - 2p_2 + p_2^2) \\ &= p_{22} - p_2^2 \end{aligned}$$

For the later terms,

$$\begin{aligned} p_{12} - p_1p_2 &= p_2 - p_{22} - (1 - p_2)p_2 \\ &= -(p_{22} - p_2^2) \end{aligned}$$

thus,

$$a = 4(p_{22} - p_2^2) \tag{9}$$

Finally,

$$\begin{aligned} c &= p_2 - (1 - p_2) \\ &= 2p_2 - 1 \end{aligned} \tag{10}$$

Relating the indices

We now form the sum

$$\begin{aligned} a + c^2 &= 4(p_{22} - p_2^2) + (2p_2 - 1)^2 \\ &= 4p_{22} - 4p_2^2 + 4p_2^2 - 4p_2 + 1 \\ &= 1 - 4(p_2 - p_{22}) \end{aligned}$$

thus,

$$s = a + c^2 \tag{11}$$

We see, therefore, that stability is the sum of contributions from acute bias and chronic bias. Further, since a square cannot be negative, the presence of chronic bias must increase stability: any imbalance between p_1 and p_2 will increase the probability of repeating percepts, regardless of the direction of the imbalance. Acute bias can, however, increase or decrease stability depending on whether a percept increases or decreases the probability that the following percept is the same.

Index limits

In comparing effect sizes, it is useful to know the maximum and minimum values of the indices. These are derived in Table 2, which shows extreme cases of the percept sequence. The minima and maxima for all indices are -1 and 1, respectively, which is a useful property when comparing them.

Results

When a perceptually ambiguous stimulus is presented continuously, the percept alternates between states every few seconds (Levelt, 1966; Wallach & O’Connell, 1953), whereas intermittent presentation tends to promote perceptual stability (Leopold et al., 2002; Orbach et al., 1963; Pearson & Brascamp, 2008). The mechanisms underlying this short-term bias are now quite well understood. In particular, the bias can build up and die away over the period of several presentations (Brascamp et al., 2008; Pastukhov & Braun, 2008). However, there is another factor that could lead to stability, namely, a perceptual bias that exists before the start of any stimulus sequence. The contribution of long-term bias to perceptual stability is poorly understood. We aimed to examine the influence of both short- and long-term bias in intermittent binocular rivalry.

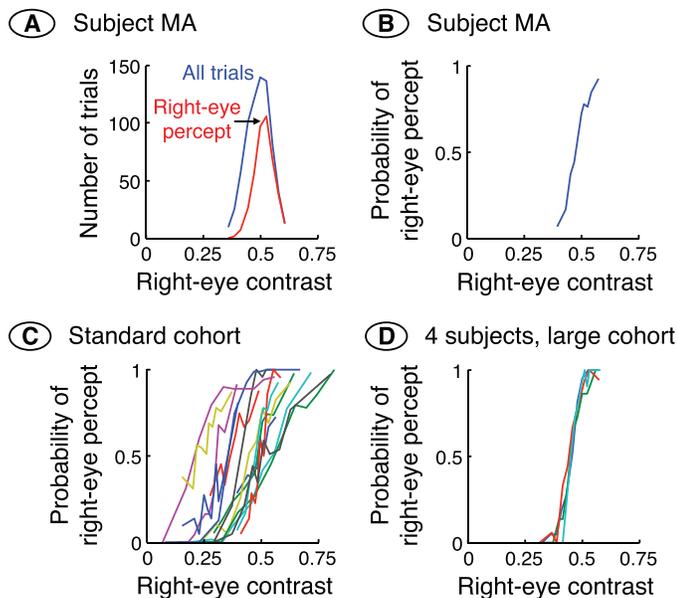


Figure 2. Psychometric functions. (A) Right-eye contrast on each trial was drawn from a Gaussian probability density; the blue curve shows the frequency histogram obtained by compiling the contrasts into 10 bins. Also shown, in red, is the frequency histogram for trials on which the subject perceived the right eye's stimulus. (B) The psychometric function was obtained by dividing the red curve (part A) by the blue curve. (C) Psychometric functions for 15 subjects in the standard cohort. Most of the data points lie in the area where right-eye contrast is less than left-eye contrast, indicating that a majority of subjects have a bias to the right-eye stimulus. (D) Psychometric functions for those subjects in the large cohort whose functions lay within the small contrast range used on this group. A bias toward the right-eye stimulus is again evident.

Chronic bias

A Gabor patch was shown to one eye and an orthogonal patch to the fellow eye, as shown in Figure 1A. The contrast of the right-eye stimulus was variable and the left eye's contrast was set so that the sum of the monocular contrasts was 1: three possible combinations are shown in the figure. On each trial the patches were present for 1 s, absent for 4 s, and subjects used the blank period to indicate the percept produced by the patches as illustrated in Figure 1B. Short blank periods encourage perceptual instability (Leopold et al., 2002), but our choice of duration avoided this problem. The duration of a run of trials was 60 s. The contrast of the Gabor presented to the right eye on each trial was drawn from a Gaussian probability density, as shown by the upper curve in Figure 2A. This graph also shows the number of trials in which the subject perceived the right eye's stimulus. Dividing the two frequency histograms yielded the psychometric function, as shown in Figure 2B.

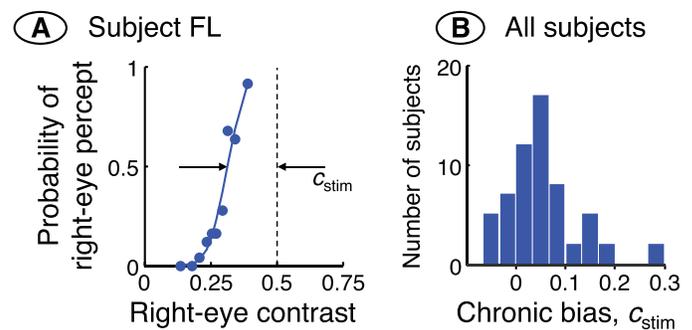


Figure 3. Quantifying chronic bias. (A) As shown for a single subject, a Gaussian distribution was fitted to the psychometric function. Chronic bias was quantified as the displacement, c_{stim} , of the fitted curve from the point at which the two monocular contrasts were equal (to 0.5). (B) The frequency histogram of chronic bias for 64 subjects in both cohorts is skewed, indicating preference for the right-eye percept.

Figure 2C shows psychometric functions from subjects in the standard cohort; the contrast range was adjusted for each subject so that the full function was obtained. Not surprisingly, the probability of seeing the right eye's stimulus tends to increase as the contrast of that stimulus is raised. Less expected is the bias of these curves toward the left side of the graph. This means that when the left-eye and right-eye stimuli have equal contrast, the right-eye stimulus is seen more often than is the left. Figure 2D shows psychometric functions from subjects in the large cohort. This cohort comprised 50 subjects, each of whom was studied for at most one hour. The data shown here are from the four subjects whose psychometric functions fell completely within the (small) range of contrasts used for this cohort. Again, these functions show dominance by the right eye's stimulus.

The bias displayed in Figures 2C and D is chronic, in that it survived many minutes of observation time. This chronic bias can be measured in at least two ways. First, there is the probability of a right-eye percept. This measure, however, varies with right-eye contrast. An alternative approach is shown in Figure 3A. Each subject's psychometric function was fitted with a Gaussian distribution and the point of subjective equality, *PSE*, was estimated as the contrast for which the fitted curve yields equal probabilities of right- and left-eye percepts. Chronic bias is then the displacement of the point of subjective equality from the point at which both monocular contrasts equal 0.5:

$$\text{chronic bias, } c_{stim} = 0.5 - PSE \quad (12)$$

The subscript, *stim*, indicates that the measurement is made in stimulus terms rather than the probability terms used below. Figure 3B shows chronic bias for subjects in both the standard and large cohorts: chronic

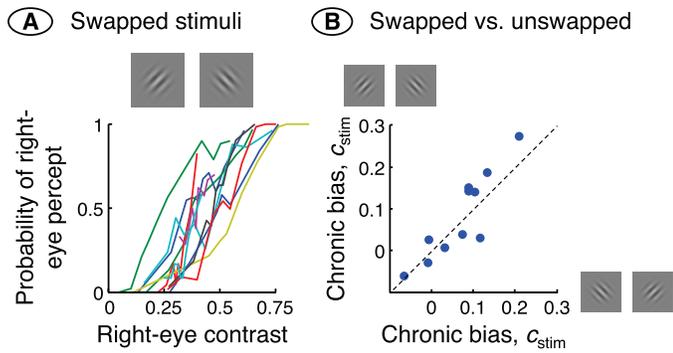


Figure 4. Source of the chronic bias. (A) The psychometric functions were recorded when the two monocular stimuli were swapped, as shown in the images above the graph. (B) The horizontal axis gives chronic bias for the monocular stimuli in their usual locations and the vertical axis gives the bias when the two stimuli are swapped, with one circle per subject. There is a significant correlation between the two variables, indicating that the bias toward the right-eye stimulus is not a bias for a specific orientation.

bias is significantly greater than zero (right-tailed sign test: $\text{sign} = 48$, $\alpha = 0.05$, $p = 3.8 \times 10^{-6}$).

This perceptual bias toward the right eye's stimulus could result from one or both of two sources: (a) a bias toward an orientation tilted rightward of vertical and (b) a bias toward a stimulus presented to the right eye. To distinguish between these two possibilities, we repeated the experiment with the two orientations swapped between the eyes, as shown in Figure 4A. Data come from only the standard cohort because there was insufficient time to perform this experiment with the large cohort. The psychometric functions are clearly shifted to the left side, indicating a bias to the right eye's stimulus. Figure 4B plots bias for swapped orientations against those for the original experiment; the correlation here is statistically significant (correlation coefficient = 0.89, $\alpha = 0.05$, $p = 0.00020$). We conclude that the chronic bias toward the right eye's stimulus is due to ocular dominance rather than orientation preference. As described in the Discussion, right-eye dominance is a common finding in a variety of binocular rivalry experiments.

Perceptual indices

Intermittent presentation of ambiguous stimuli can lead to perceptual stabilization. There are two contributors to stability. First, there is a short-term effect, in which one percept depends in some way on the preceding percepts. Second, a long-term bias to one percept can also lead to stability: the favored percept will appear more often regardless of any short-term

effects. To understand perceptual stability we need to separate these two contributors, chronic and acute bias. The Methods section provides a detailed mathematical analysis of this separation; we here provide an overview of the analysis so that the essential variables can be easily understood. The separation is most easily performed by assuming the simplest case, namely that the presentation of an ambiguous stimulus leads to either of two percepts, 1 or 2. We define indices for each of stability, acute bias and chronic bias, such that the index is zero when the corresponding effect is absent. *Stability* is defined as

$$\begin{aligned} \text{stability, } s &= \text{probability that two consecutive} \\ &\quad \text{percepts are the same} \\ &\quad - \text{probability that they differ.} \end{aligned} \quad (13)$$

Acute bias refers to serial dependence between percepts and can be measured by subtracting out the contribution due to independence of percepts:

$$\begin{aligned} \text{acute bias, } a &= s - \text{value of } s \text{ when consecutive} \\ &\quad \text{percepts are independent.} \end{aligned} \quad (14)$$

The second term in this equation is the degree of stability expected if each percept is independent of the preceding percept, which is simply the product of the probabilities of the individual percepts. Finally, *chronic bias* is a property of single percepts:

$$\begin{aligned} \text{chronic bias, } c &= \text{probability of percept 2} \\ &\quad - \text{probability of percept 1.} \end{aligned} \quad (15)$$

The three indices are rigorously defined in the Methods. It is shown there that a relationship exists between them:

$$s = a + c^2. \quad (16)$$

This equation tells us two things. First, stability is the sum of two components, one from acute bias and the other from chronic bias. Second, these two components differ in an important way. The acute bias is positive if serial dependence increases the probability that one percept is the same as the previous one, and is negative if it decreases that probability. Chronic bias can only increase stability, however, because its contribution is squared.

Each index is defined so that it is zero in the absence of the effect it measures, has a maximum value of 1, and has a minimum of -1 . Negative stability, for example, occurs when one percept tends to be followed by the other percept and negative acute bias indicates that this percept sequence is due to serial dependence. Negative chronic bias indicates that percept 1 is more likely than percept 2. The sharing of common limits makes it easy to compare one effect size with another.

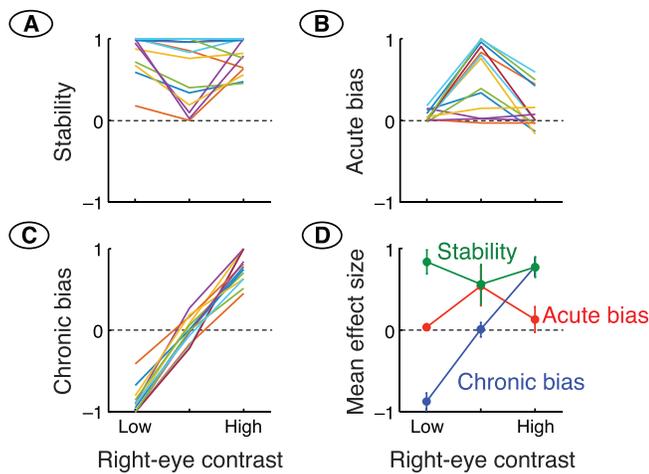


Figure 5. Indices of perceptual stabilization. A subset of the data already described was analyzed by choosing those pairs of consecutive trials in which the two contrasts were similar. Specifically, contrasts were sorted into three bins: the middle bin was centered on the contrast that produced equally probable right- and left-eye percepts, and contained one third of trials. The 35% of trials pairs for which the contrasts fell into different bins were discarded. (The rejection rate is lower than the 67% expected of a 3×3 experimental design because the middle bin was typically off-center in the contrast range.) (A) The vertical axis indicates the index of stability and each line represents a subject in the standard cohort. Stability is positive, indicating that a percept on a trial tended to be the same as that on the previous trial. (B, C) Acute bias is the component of stability that results from correlation of consecutive percepts, and chronic bias is the bias to the right-eye percept regardless of perceptual history. (D) This graph shows mean effect sizes over all the subjects analyzed, and error bars provide 95% confidence intervals. Acute bias is high only when chronic bias is close to zero, for the middle contrast bin.

Measuring the indices

We put the theory to a test with the same data set used to measure chronic bias. For any given subject, the most interesting range of right-eye contrasts is centered on the contrast that nulls the subject's chronic bias. As described above, right-eye contrast was therefore sampled from a Gaussian probability density centered on a value that nulls a subject's bias and left-eye contrast was set so that the sum of monocular contrasts was 1. The results for 12 subjects are shown in Figure 5. The figure shows only those pairs of consecutive percepts for which both contrasts fall into low, medium, or high bins. Figure 5A shows that stability is positive across the contrast range, and Figure 5C shows that the percept is dominated by the left- and right-eye stimuli when right-eye contrast is low and high, respectively. The acute bias, in Figure 5B, is only strong when chronic bias is not. Figure 5D gives the mean over all these subjects, and

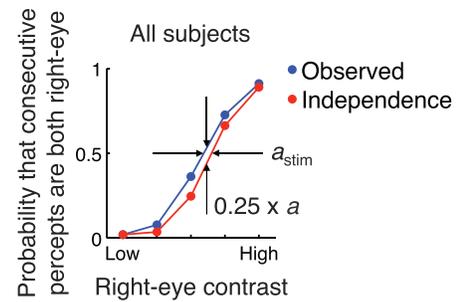


Figure 6. Acute bias measured in stimulus terms. All the percept pairs in Figure 5 were sorted into five contrast bins, and analyzed to find the probability that both percepts were of the right-eye stimulus. Trials were binned in two steps: (1) The middle bin was centered on the contrast that produced equally probable right-eye and left-eye percepts, and contained one fifth of the trials; and (2) The two lowest bins contained equal numbers of trials, as nearly as possible, as did the two highest bins. The circles give means over all analyzed subjects. The blue curve gives observed probability (p_{22} in the terminology of Equation 9) and the red curve the probability assuming that percepts on the two trials are independent (that is, p_2^2). The horizontal distance between the two curves gives acute bias in stimulus terms, and the vertical distance is proportional to the acute bias in terms of probability.

95% confidence intervals. The middle bin indicates that perceptual stability is entirely due to the correlation of consecutive percepts when the effects of chronic bias are removed. For the bin with high right-eye contrast, chronic bias is significantly greater than zero, whereas acute bias is not.

Acute bias

We can learn more about the acute bias by breaking it down into components. It is shown in the Methods section that acute bias,

$$a = 4 \times (p_{22,observed} - p_{22,independence}). \quad (17)$$

The first component, $p_{22,observed}$, is the observed probability that percept 2 is experienced on two consecutive trials. The second component, $p_{22,independence}$, is the value of this probability when the two percepts are independent. Figure 6 shows both the probabilities as a function of right-eye contrast; values are means over 13 subjects. The vertical distance between the curves equals one quarter of the acute bias, and clearly varies with the contrast used. An alternative approach to measuring the index is also shown. The lateral distance between the two curves provides a value for the acute bias, a_{stim} , in terms of the stimulus rather than probability. This measure has the advantage that it is largely independent of the contrast used to measure it.

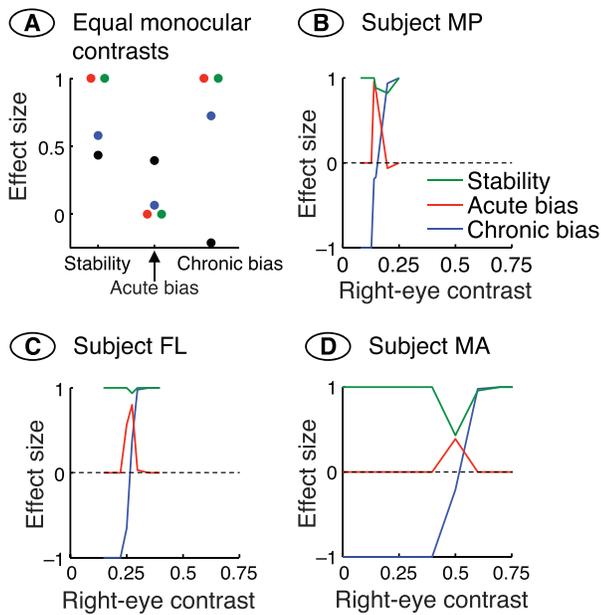


Figure 7. Stabilization indices measured with constant contrasts. This figure shows the indices measured with constant contrast on a subset of subjects in the standard cohort. (A) Measurements with equal monocular contrasts on four subjects, with each subject represented by a different color. Chronic bias tends to outweigh acute bias. (B–D) Each graph shows one subject. Stability is high at all contrasts and acute bias is only high where chronic bias is close to zero. These results are consistent with those in Figure 5.

Constant contrast

The preceding results used stimulus contrasts that varied from trial to trial. This is an unusual approach because most studies of perceptual stability use stimuli that are fixed in strength throughout a run (e.g., Leopold et al., 2002). We therefore checked our conclusions on a sample of subjects stimulated with constant contrasts. Figure 7A shows the perceptual indices for four subjects when the monocular contrasts were both set to 0.5. Stability is positive for all subjects, as expected. Chronic bias is maximal or near maximal for three out of these four subjects (i.e., their percepts are strongly dominated by the right eye) and acute bias is therefore close to zero. The extent to which the bias existed before the start of the run, or built up during the run (Brascamp et al., 2008; Pastukhov & Braun, 2008), is not obvious here: this is an issue taken up in the Discussion. In further runs, right-eye contrast was reduced to lessen the right-eye domination. Figure 7B, C, and D show the results for three subjects. Stability is positive at all tested contrasts, indicating perceptual stabilization. Chronic bias is negative at the left side of each graph, indicating that the dominant percept is the left-eye stimulus, and positive at the right side where the right-eye stimulus dominates. The right-eye con-

trast required to null chronic bias, however, differs widely between subjects. Subject MP's responses are strongly dominated by the right-eye stimulus, for which contrast had to be set at about one quarter of left-eye contrast to null chronic bias. For subject MA, by comparison, chronic bias is close to zero when the two monocular contrasts are equal. Given that stability is a sum of acute and chronic effects, acute bias is only positive when chronic bias is largely nulled. The findings here therefore confirm the results obtained with variable contrast.

Continuous rivalry

Given the chronic bias found during intermittent binocular rivalry, we were curious whether the same bias would be evident during continuous rivalry. For this experiment, subjects viewed the orthogonal Gabor stimuli continuously and signaled the onset of three possible percepts: left-eye stimulus, right-eye stimulus, or a mixture of the two. The probability of the right-eye percept was calculated as the duration of this percept divided by the sum of the times for which the left- or right-eye stimulus was seen. As before, the left- and right-eye contrasts were set so that their sum was 1. Right-eye contrast was not randomized; it was fixed at a multiple of 0.1 for the whole of each run.

Figure 8A shows the resulting psychometric functions for those 11 standard cohort subjects who were available for the experiment. Not surprisingly, the probability of the right eye's percept climbs with right-eye contrast. More to the point, most of the curves are shifted left of center, suggesting a right-eye bias. To test this suggestion, a Gaussian distribution was fitted to the data as shown in Figure 8B and chronic bias was calculated in stimulus terms using Equation 12. Figure 8C shows that the chronic bias is greater than zero for most subjects. The number of subjects, however, was insufficient to test for significance. To include the large cohort of subjects, we had to modify our approach because each subject in that cohort was examined for only one hour, which is insufficient to record a complete psychometric function. Instead, we measured the chronic bias in probability terms when both monocular contrasts were set to 0.5, as shown in Figure 8B. Chronic bias is shown in Figure 8D. This frequency histogram indicates that the chronic bias is significantly greater than zero (right-tailed sign test: $\text{sign} = 43$, $\alpha = 0.05$, $p = 0.0041$). We conclude that, just as with intermittent rivalry, there is a bias toward the right-eye's stimulus during continuous rivalry.

While intermittent and continuous rivalry share an ocular bias, we also found a clear difference between these two forms of rivalry. Compare Figure 2C and Figure 8A: the psychometric function during continu-

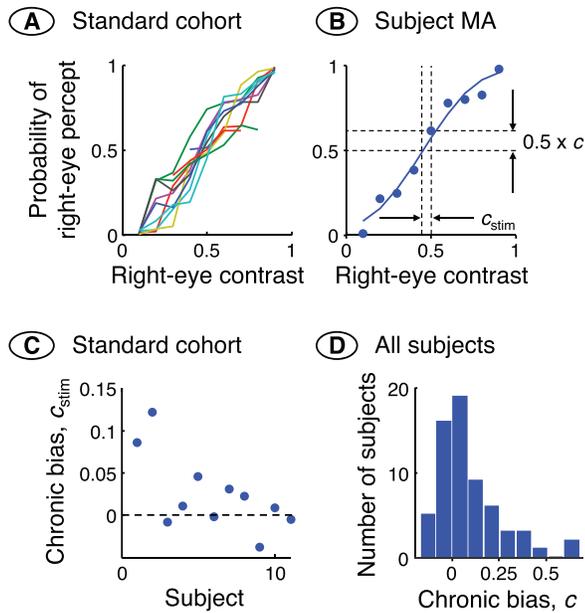


Figure 8. Continuous binocular rivalry. The stimulus in Figure 1 was presented continuously, rather than intermittently, and subjects continuously indicated the percept. (A) The vertical axis indicates the duration of right-eye percepts divided by the sum of durations in which the percept was either right- or left-eye. As expected, the probability of a right-eye percept climbs with right-eye contrast. Each line represents one subject in the standard cohort. (B) Chronic bias toward the right eye was measured by fitting a Gaussian distribution to the observations. The horizontal displacement of the model from the contrast at which the monocular contrasts are equal (to 0.5) gives chronic bias in stimulus terms, c_{stim} . The vertical displacement from the point at which the two percepts are equally probable is proportional to chronic bias, c , expressed in probability terms. (C) Chronic bias in stimulus terms for each analyzed subject. The bias is generally positive, indicating a bias to the right-eye percept. (D) Chronic bias in probability terms for all subjects in both cohorts. The bias is significantly positive.

ous rivalry has a lower slope than that recorded during intermittent rivalry. Figure 9 provides a direct comparison between the two forms of rivalry. Chronic bias, shown in Figure 9A, is usually greater than zero, regardless of the type of rivalry. The psychometric function slopes, in Figure 9B, fall into two clearly separable groups: taking the logarithm of slope (to make the probability densities similar for the two groups) shows that the two medians are significantly different (right-tailed Wilcoxon rank sum test: rank sum = 285, $\alpha = 0.05$, $p = 1.0 \times 10^{-5}$). Psychometric slope decreases as neural signals become noisier (Pelli, 1985), suggesting that noise plays a greater role during continuous rivalry. This is an issue taken further in the Discussion.

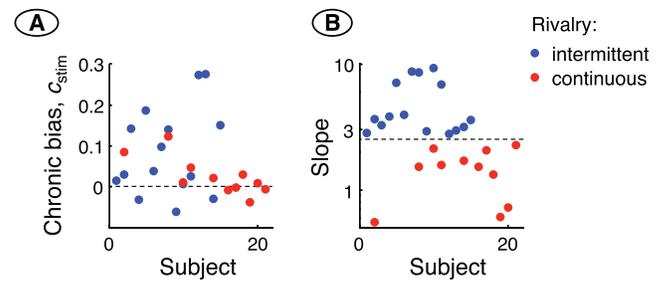


Figure 9. Comparison between intermittent and continuous rivalry. Each circle represents one subject in the standard cohort; intermittent rivalry is shown in blue and continuous rivalry in red. (A) Chronic bias in stimulus terms tends to be positive, indicating a bias to the right eye, but values from the two types of rivalry are mingled. (B) The slope of the psychometric function is higher in intermittent rivalry (the dashed line separates the two types of data), indicating that noise may play a smaller role in intermittent than in continuous rivalry.

Discussion

We have described four key new findings in this paper.

- Perceptual stability during ambiguous stimulation results from both chronic and acute biases.
- Stability can be expressed as a sum of contributions from chronic and acute bias.
- There is a pronounced chronic bias toward the right eye's stimulus during both intermittent and continuous binocular rivalry.
- Varying the relative strength of the rivaling stimuli varies the relative contributions of chronic and acute bias to perceptual stability.

Chronic biases, which thread through these new findings, are commonly found in ambiguous stimuli. Using pooled data from several previous studies of binocular rivalry, Porac and Coren (1976) showed that 48% of subjects in the sample preferred the right eye, 32% the left eye, and the remainder were ambicular. When subjects were asked to align near and distant targets in a sighting task, about two thirds used their right eye (Ehrenstein et al., 2005; Porac & Coren, 1976). Several studies have noted a chronic bias toward one eye or the other at the onset of binocular rivalry (Carter & Cavanagh, 2007; de Jong et al., 2012; Stanley et al., 2011). Further, chronic bias is not limited to binocular rivalry: Knapen et al. (2009) and de Jong et al. (2012) noted strong subject-specific bias to one direction of rotation at the onset of stimulation with a structure-from-motion task, and Sundareswara and Schrater (2008) found a strong bias to the view from above in subjects shown the Necker cube.

We have separated bias into two components, acute and chronic. By our definition, acute bias indicates the dependence of one percept on the previous one, whereas chronic bias indicates any component of bias that cannot be attributed to such lag-one dependence. It has been shown that perceptual stability builds up over a succession of percepts before the current one (Brascamp et al., 2008; Pastukhov & Braun, 2008). It is therefore possible that our chronic bias term includes preexisting effects, as well as effects that accumulate between the start of a run and the percept two back from the present. The contribution of such cumulative effects is minimized in our experiments, however, given our experimental design. We used runs of shorter duration (60 s) than those used in previous work, in which runs of many minutes are commonplace. This means that one percept, that produced by preexisting bias in particular, dominated complete runs in our data, whereas longer runs can produce an eventual switch to the alternate percept (e.g., Leopold et al., 2002). In our constant-contrast runs, for example, 27% of runs contained only one percept. To a considerable extent, therefore, our measure of chronic bias reflects an effect present before the start of a run. This conclusion is reinforced by two other observations. First, for most (75%) of the subjects, the data were recorded over two or more days, meaning that chronic bias survives over that period. Second, the bias is almost always toward the right eye, a very unlikely observation if it arose only from effects that accumulate during a run.

Intermittent rivalry and continuous rivalry clearly differ in their properties, and the most obvious difference is in their time courses. The perceptual stability induced by intermittent rivalry can last many minutes and survives for at least a minute between one period of stimulation and the next (Leopold et al., 2002). By comparison, in continuous rivalry the percept changes every few seconds. This difference raises the possibility that the neural populations subserving the two types of rivalry may also differ. There is psychophysical evidence that binocular rivalry is initiated in or near primary visual cortex (Freeman & Li, 2009), and magnetic resonance imaging shows strong effects of rivalry in the same area (Polonsky, Blake, Braun, & Heeger, 2000). Further, single-neuron responses increasingly correlate with rivalry percepts as signals progress downstream from primary visual cortex (Sheinberg & Logothetis, 1997). What, then, is the neural locus for the stabilization seen in intermittent rivalry? Our results offer a clue. It is known that contrast-response functions grow steeper from primary to higher visual cortex (Avidan et al., 2002; Sclar, Maunsell, & Lennie, 1990). Correspondingly, we find that the psychometric function for intermittent rivalry is significantly steeper than that for continuous rivalry,

suggesting that intermittent rivalry may be subserved by neural populations at the downstream end of those involved in continuous rivalry. This suggestion awaits neurophysiological confirmation.

Keywords: ambiguous perception, perceptual stabilization, bias

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