



Minireview

The ‘laws’ of binocular rivalry: 50 years of Levelt’s propositions

J.W. Brascamp^{a,*}, P.C. Klink^{b,c,d} with a contribution from W.J.M. Levelt^e^a Helmholtz Institute and Division of Experimental Psychology, Department of Psychology, Utrecht University, Utrecht, The Netherlands^b Vision & Cognition, Netherlands Institute for Neuroscience, Royal Netherlands Academy of Arts & Sciences, Amsterdam, The Netherlands^c Neuromodulation & Behaviour, Netherlands Institute for Neuroscience, Royal Netherlands Academy of Arts & Sciences, Amsterdam, The Netherlands^d Department of Psychiatry, Academic Medical Center, University of Amsterdam, The Netherlands^e Max Planck Institute for Psycholinguistics, Nijmegen, The Netherlands

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ABSTRACT

It has been fifty years since Levelt’s monograph *On Binocular Rivalry* (1965) was published, but its four propositions that describe the relation between stimulus strength and the phenomenology of binocular rivalry remain a benchmark for theorists and experimentalists even today. In this review, we will revisit the original conception of the four propositions and the scientific landscape in which this happened. We will also provide a brief update concerning distributions of dominance durations, another aspect of Levelt’s monograph that has maintained a prominent presence in the field. In a critical evaluation of Levelt’s propositions against current knowledge of binocular rivalry we will then demonstrate that the original propositions are not completely compatible with what is known today, but that they can, in a straightforward way, be modified to encapsulate the progress that has been made over the past fifty years. The resulting modified, propositions are shown to apply to a broad range of bistable perceptual phenomena, not just binocular rivalry, and they allow important inferences about the underlying neural systems. We argue that these inferences reflect canonical neural properties that play a role in visual perception in general, and we discuss ways in which future research can build on the work reviewed here to attain a better understanding of these properties.

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1. Introduction

Binocular rivalry is the striking phenomenon that ensues when the two eyes view markedly different stimuli: the observer perceives only one stimulus at a time, and perception alternates between the two stimuli at irregular intervals. The first systematic study of the phenomenon dates back to Sir Charles Wheatstone’s invention of the stereoscope in 1838 (Wheatstone, 1838; reviewed by Blake, 2005), and while the paradigm might currently best be known as a valuable tool to study the mechanisms of visual awareness, earlier studies primarily focused on its relation to binocular visual processing and on the question why rivalry occurs in the first place. Without disputing the relevance of binocular rivalry as an experimental tool to dissociate the input to visual processing (physical stimuli) from its output (conscious perception), it must be noted that despite a long and rich history of binocular rivalry research, the actual mechanisms that give rise to the phenomenon are still not entirely understood today (Blake & Wilson, 2011; Sterzer, Kleinschmidt, & Rees, 2009; Tong, Meng, & Blake, 2006).

Among the many experimental investigations of the binocular rivalry mechanism, there are few studies that have had such a lasting influence on the field as Levelt’s monograph *On Binocular Rivalry*, published half a century ago this year (Levelt, 1965¹). The monograph, essentially a write-up of Levelt’s PhD work, covers several topics, but the main reason for its enduring importance is its description of four *propositions* that formalize central aspects of binocular rivalry’s phenomenology. By capturing a rich array of experimental findings in a concise set of rules, these propositions have been of tremendous value to the field. They serve as the main reference point for theorists aiming to capture in formal models the neural interactions that underlie binocular rivalry. For experimentalists, the propositions provide a unifying framework that guides interpretation of an ever-growing set of observations.

On the occasion of the monograph’s 50th anniversary this mini review will revisit the origins of the four propositions and evaluate the propositions against a summary of the progress the field has made since then. After a brief description of the propositions, the narrative will continue as follows. In the first section Willem

* Corresponding author.

E-mail address: j.w.brascamp@gmail.com (J.W. Brascamp).¹ A digital version of the complete monograph can be found here: http://www.mpi.nl/world/materials/publications/levelt/Levelt_Binocular_Rivalry_1965.pdf.

Levelt will sketch the scientific landscape that supported the propositions' conception, thereby touching on aspects of the 1965 work that formed the propositions' original context but that may not be at the forefront of researchers' minds today. Next we will review the accumulation of knowledge in this field since 1965, and identify where modifications to the original propositions are required. We will attempt to formulate a concise set of modified rules, firmly based on the original propositions but adjusted to our current understanding of binocular rivalry. In the subsequent section, we will summarize striking recent evidence implying that these updated propositions, although formulated within the context of binocular rivalry, are applicable to a much broader set of bistable perceptual phenomena. We will then also briefly touch on current knowledge concerning another element of the 1965 monograph that has remained in the spotlight as a hallmark of binocular rivalry, namely the distribution of perceptual dominance durations. In the next section we will discuss what the propositions and associated work convey about the characteristics of the neural systems responsible for bistable perception, and we will argue that these are general characteristics that recur throughout the visual brain. The final section will suggest possible ways for future work to investigate these characteristics by building on the results we review here.

It should be mentioned that JWB and PCK performed the critical assessment of the 1965 work against current knowledge of the binocular rivalry phenomenon, and wrote the initial version of the corresponding part of the paper. Before writing, WJML was approached to provide the section on the historical context to his original work, an invitation he kindly accepted. All authors then jointly designed the structure of the manuscript and all three contributed to all manuscript sections as part of the internal revision cycle.

2. The four propositions

Levelt's propositions document key aspects of the way in which perception during binocular rivalry depends on characteristics of the stimuli involved. Before we can continue to the propositions themselves there are a few concepts, both associated with the stimuli and with the perceptual experience, that require formal definition. A useful concept of the former kind, that Levelt introduced when he formulated his propositions, is *stimulus strength*. Each monocular stimulus engaged in binocular rivalry can be characterized in terms of its stimulus strength, and this variable affects binocular rivalry between the two images. As detailed in the next section, when Levelt introduced the concept of stimulus strength, he considered the variable to be determined by the contrast, density and blur of the contours that make up an eye's stimulus, and he had a direct link in mind with the contribution of that same stimulus, during fusion, to binocular brightness perception. Nowadays, it is common to think of stimulus strength purely in terms of binocular rivalry, and to interpret it to mean, quite generally, the degree to which the physical characteristics of one eye's stimulus enable that stimulus to perceptually suppress the stimulus presented to the other eye. As reviewed below, there is a remarkable range of distinct stimulus manipulations whose effects can be coherently described using this single, broad concept of stimulus strength, and only few cases so far have suggested a need for characterizations that allow more specific distinctions between various kinds of manipulations.

The remaining concepts that we will define here pertain to the perceptual experience during binocular rivalry. During rivalry, each eye's stimulus will be perceived for a certain *dominance time*, before it is perceptually replaced by the other eye's stimulus. This process of *perceptual alternations* can be characterized by the

alternation rate: the number of perceptual alternations within a predefined time window. For each eye's stimulus one may further calculate the *predominance* as the total proportion of the binocular rivalry viewing time that a stimulus is dominant, and the *average dominance duration* of all the individual dominance periods.

With these concepts in hand, we can now turn to the propositions. As will be discussed in more detail later, Propositions I–III are interrelated statements about the effect of changing the stimulus strength of only one monocular image during rivalry, whereas Proposition IV is an independent description of the effect of changing both images. The original propositions can be paraphrased as follows:

- I. Increasing stimulus strength for one eye will increase the perceptual predominance of that eye's stimulus.
- II. Increasing stimulus strength for one eye will not affect the average perceptual dominance duration of that eye's stimulus. Instead, it will reduce the average perceptual dominance duration of the other eye's stimulus.
- III. Increasing stimulus strength for one eye will increase the perceptual alternation rate.
- IV. Increasing stimulus strength in both eyes while keeping it equal between eyes will increase the perceptual alternation rate.

How did these propositions, quite familiar to many present-day binocular rivalry scholars, originally come into being? Our next section will answer this question by providing a birds-eye view of the reasoning followed in [Levelt's \(1965\)](#) monograph.

3. The 1965 context, findings and theory

What causes the perceptual conflict in binocular rivalry? That was the core issue addressed in [Levelt \(1965\)](#). Why do the two images presented to the individual eyes not add or average as seems to be the case in normal fusion? Two centuries earlier, [Du Tour \(1760\)](#) had suggested that observers always perceive only one eye's image or the other's, not a combination of both – conflicting input, according to Du Tour, makes this ordinarily inconspicuous rivalry noticeable. While later evidence argued against this *permanent rivalry hypothesis* ([Blake & Camisa, 1978](#); [Kang, Heeger, & Blake, 2009](#)), it was still a core issue in the 1965 context. Explaining the cause of conflict in rivalry was also considered relevant for the debate concerning the mechanism of binocular fusion. [Hering \(1864\)](#) had aligned himself with the permanent rivalry hypothesis, stating that if the eyes are presented with similar fields that differed in brightness, perception does not reflect the sum of these fields, but the two compete in the binocular field. According to him, the result is

“... that, if we call the resulting sensation unity, both retinas have approximately complementary shares in the production of the sensation, i.e. if the contribution of one retina is 3/4, then the contribution of the other one is 1/4. If one contributes 1/2, then the other also contributes 1/2, and if one gives 1, the other gives 0. Perhaps we have to assume that, if both retina's are stimulated absolutely equally, they will have equal shares (i.e. 1/2) in the common visual field” (p. 310).

But even then, there is an underlying rivalry according to Hering. The ‘whites’ of the two retina's dominate in turn. During the transition phases

“part of the white of one retina is mixed with part of the white of the other one, in such a way that the ratio of the two shares in the resulting view keeps being rather constant, as shown by experience. We would in this way see a mixed white as it were,

which of course can in no way be distinguished from the simple white which we see when only the white of one retina is expressed in the visual field.” (p. 309).

Hering also adopted Meyer’s (1855) law, which states that contours are absolutely dominant in binocular interaction and that it is their competition that makes depth perception possible:

“Binocular depth perception . . . is only possible through retinal rivalry and the victory of contours.” (p. 315)

The mechanisms of binocular brightness interaction and contour dominance were to form the ingredients of Levelt’s (1965) account of the perceptual conflict in rivalry. A first set of experiments measured equibrightness curves for binocular white test disks on black backgrounds (Fig. 1A), associated with Hering’s ideas on the perception of binocular luminance fields. The experimenter set the luminance of the left (or right) test disk and observers adjusted the luminance of the right (or left) disk in such a way as to match the brightness impression of this test pair to a constant comparison pair equal in luminance presented to both eyes. Observers could look back and forth at the test and comparison until a satisfactory match had been obtained. Fig. 1A presents a characteristic brightness curve obtained in such way. The two tails of the curve show “Fechner’s paradox”, a known phenomenon defined as the subjective impression of lower brightness during binocular presentation compared to monocular presentation, even though the total amount of light that enters the two eyes is higher in the binocular condition. The linear portions of the curves obtained could be expressed in a straightforward equation (Eq. (1))

$$C = w_l E_l + w_r E_r \tag{1}$$

In this equation, E_l and E_r denote luminances (energies), w_l and w_r are weighting coefficients accounting for the subject’s eye dominance, and C is a constant.

The next set of experiments measured the other pertinent mechanism in rivalry, the effect of a monocular contour on binocular brightness, associated with Meyer’s law. The experimental procedure was exactly the same as in the first set of experiments, but there was a small change in stimuli. Whereas both test stimuli contained a concentric circle in the former case (Fig. 1A), in the new experiment only one eye’s image, either the left or the right one, contained a circle (Fig. 1B). The comparison stimuli both contained the circle. Characteristic equibrightness curves (for the same observer) are presented in Fig. 1B. Apparently, the introduction of a mere contour in one but not the other eye induces a shift in weighting coefficients of the two eyes, but their sum is still constant. The eye-related contributions can be expressed as proportions: $w_l + w_r = 1$. This finding was coined “The law of complementary shares” in recognition of Ewald Hering.

A further set of experiments was designed to test the limits of this proportional shift. This was done by varying the size of the test disk in one eye, while presenting the other eye with a large homogeneous test field. The smaller the test field, the closer its area is to its outer contour. Varying the size of the monocular test field from 7 to 5, 3 and 1 degree of visual angle, the contribution of that test field to the binocular brightness impression increased (over 8 observers) from $w = .851$ to $.857$ to $.887$ to $.932$. In other words, a half-image’s contribution to binocular brightness approaches $w = 1$ when its average distance to a contour approaches zero. This was coined the “contour mechanism”. The perceived brightness remains quite stable for all sizes of the test

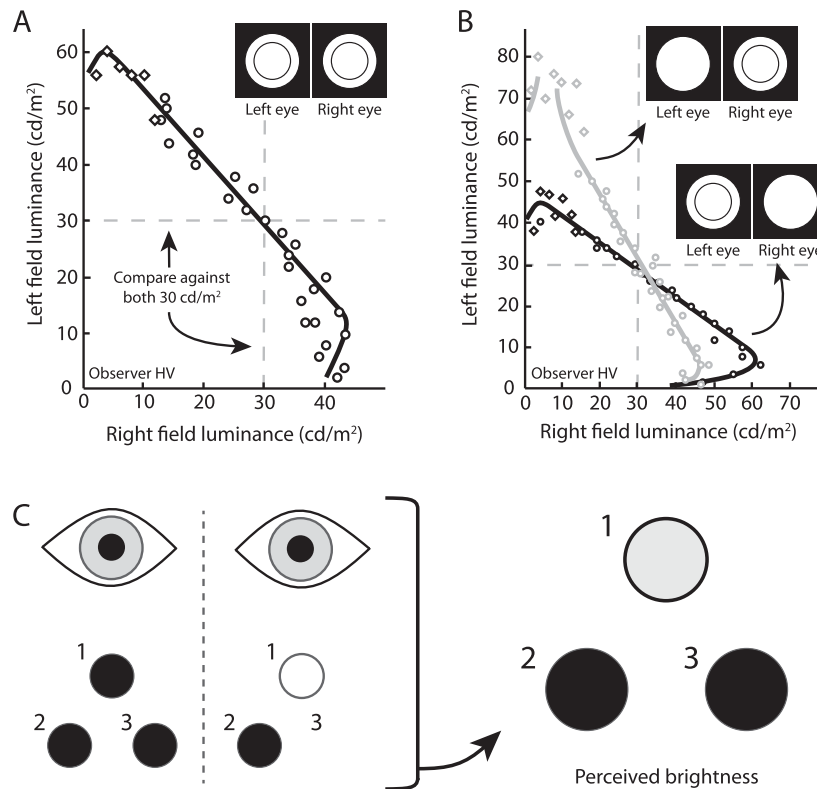


Fig. 1. Binocular equibrightness measurements. (A) Pairs of fused disks (inset) containing a concentric circle were used both as test and as comparison stimuli to measure and construct equibrightness curves (here for one observer, HV). Test stimuli were compared against a binocular comparison field luminance of 30 cd/m². (B) Equibrightness curves for the same observer with monocular contour in one of the two eyes. The comparison stimuli both contained an inner circle. Gray and black equibrightness curves for comparison stimuli with concentric circle in left and right eye’s stimulus respectively. (C) Classroom demonstration of the law of complementary shares. When the two half-fields are stereoscopically fused, disk 1 is perceived as considerably brighter than disk 3, even though their luminances are identical in the left and in the right half field. Disk 1, however, has a contour in both half-fields, inducing $w_l \approx w_r \approx 1/2$ whereas disk 3 has a contour in the left half-field only, inducing $w_l \approx 1, w_r \approx 0$. Disks 2 and 3 are not very different in perceived brightness even though disk 2 is black and disk 3 is white in the right half-field. Images adapted from Levelt (1965).

field, i.e. it is subject to a “constancy rule”. A summary classroom demonstration of all these brightness averaging effects can be experienced by fusing the stereo pair in Fig. 1C.

In additional experiments it was then shown that it takes time for the eye weighting coefficient to settle after stimulus onset. In other words, the contour mechanism shows some degree of inertia. It takes about 100–200 ms for an appearing contour to induce $w = 1$ in its immediately adjacent visual field. This delay predicts that a pair of orthogonal gratings, the classic demonstration stimulus for binocular rivalry, should look like a grid (commonly referred to as a *plaid*) if briefly flashed on and off. That indeed turned out to be the case, indicating that temporarily $w_l = w_r = 1/2$. This settling mechanism is the same as what can be observed and precisely measured in metacontrast (Alpern, 1952; Stigler, 1910) and in “false fusion” (Wolfe, 1983).

Together, these experimental findings led to the following account of the conflict in binocular rivalry. The law of complementary shares and the contour mechanism necessarily come into conflict for any dichoptic area A where adjacent but non-corresponding contours are presented to the two eyes. The contour mechanism for the left eye induces, with some degree of inertia, $w_l \rightarrow 1$ in area A_l ; the contour mechanism for the right eye similarly induces $w_r \rightarrow 1$ in area A_r . This, however, violates the law of complementary shares ($w_l + w_r = 1$). The system apparently resolves this conflict by abrogation of the constancy rule, while preserving the law of complementary shares: both $w_l \rightarrow 1$ and $w_r \rightarrow 1$, but they do so *in turn*, steadily alternating. In addition, there was no pressing reason to assume that this process would be different for the normal fused state in binocular vision. The still dominant “permanent rivalry hypothesis” was not challenged, but rather supported by this account for the conflict in binocular rivalry.

The contour mechanism, a contour inducing $w = 1$ for its immediately adjacent visual field, also formed the starting point for the analysis of the alternation process in rivalry. If a contour is presented to one eye only, the resulting percept will be stable, whatever the strength (formally denoted by λ) of that stimulus may be (not considering “Troloxer’s fading”, which was shown to be irrelevant for the rivalry mechanism). The only way to make such a stimulus perceptually disappear is by presenting a strong enough stimulus to the other eye. This notion led to the hypothesis that the duration of a monocular contour’s dominance period in rivalry is determined by the strength of a contour in the corresponding area of the other eye. This had never been studied before. Since Breese (1909), there existed a literature on the *alternation rate* in rivalry that showed that increasing luminance, contrast or amount of contours in one or both eyes increased alternation rate. There also existed an even larger literature on factors affecting the *predominance* of monocular patterns in rivalry (following Breese, 1909 and Roelofs & Zeeman, 1919), which was affected by the same or similar factors as alternation rate, in particular by the contrast or sharpness of contours. However, at the time no explicit model had been proposed to relate the two, alternation rate and predominance, to each other. Four propositions were intended to fill this gap (Levelt, 1965). In their formal description, they involved a number of symbols: \bar{t}_l and \bar{t}_r , denote the mean durations of the left and right eye dominance periods in a two-choice rivalry situation, where the mean duration of the complete cycle is $\bar{T} = \bar{t}_l + \bar{t}_r$. Predominance (p_l) of left-eye stimulus (S_l) is calculated as $100\bar{t}_l/(\bar{t}_l + \bar{t}_r)\%$ and similarly so for the right eye stimulus (S_r). Stimulus strengths of S_l and S_r are given by λ_l and λ_r respectively. Operationally, stimulus strength was defined (up to order relations) by two variables: (i) the amount of contour per area, and (ii) the contrast of contour (taking into account the local difference threshold). The above hypothesis can now be stated as $\bar{t}_l = f(\lambda_r)$ and $\bar{t}_r = f(\lambda_l)$, where f is a monotonic decreasing function of λ .

These two equations together yielded Levelt’s (1965) four propositions in their original form:

- I. Increase of the stimulus strength in one eye will increase the predominance of the stimulus.
For the left stimulus S_l , for instance, this means that $p_l = 100\bar{t}_l/(\bar{t}_l + \bar{t}_r)\% = 100\bar{t}_l/(f(\lambda_r) + \bar{t}_r)\%$. Increasing left eye stimulus strength λ_l will decrease $\bar{t}_r = f(\lambda_l)$ and hence increase p_l .
- II. Increase of the stimulus strength in one eye will not affect the average dominance duration for the same eye.
This follows from the exclusive formulation of the two equations above: \bar{t}_l can only be affected by λ_r , not by λ_l . The same goes for the other stimulus.
- III. Increase of the stimulus strength in one eye will increase the alternation frequency.
Proposition III also logically follows from the two equations. An increase of λ_l reduces \bar{t}_r and since λ_r and \bar{t}_l do not change, the cycle duration $\bar{T} = \bar{t}_l + \bar{t}_r$ also decreases and the alternation rate goes up.
- IV. Increase of the stimulus strengths in both eyes will increase the alternation frequency.
This is the final proposition to follow from the equations: increases of both λ_r lead to reductions of both \bar{t}_l and \bar{t}_r respectively. This in turn causes $\bar{T} = \bar{t}_l + \bar{t}_r$ to go down and the alternation rate to go up.

In 1965, when they were first proposed, the four propositions accounted (up to order relations) for all predominance and rate findings in the existing literature. Critical Proposition II had, however, never been tested before. Levelt (1965) reports two explicit tests of this proposition. In the first experiment, the difference threshold of the stimulus in one half field was varied by introducing blur (two levels), in the other experiment the degree of contrast was varied (two levels). The typical stimuli used in the two-choice rivalry tests are depicted in the inset of Fig. 2. In both tests 10 observers performed four one-minute rivalry recordings, pushing the response button as long as they saw the right eye stimulus, a black center disk. The data were exceedingly clear: blurring or diminishing the contrast of the left eye’s white center disk decreased the left eye’s predominance p_l (Proposition I), decreased the alternation rate (Proposition III), and left the left eye’s average dominance duration unchanged (Proposition II) without even a trend. In a further experiment an additional black ring was inserted around the black right-eye center disk. Adding a contour should increase stimulus strength of the right eye stimulus, as it had done

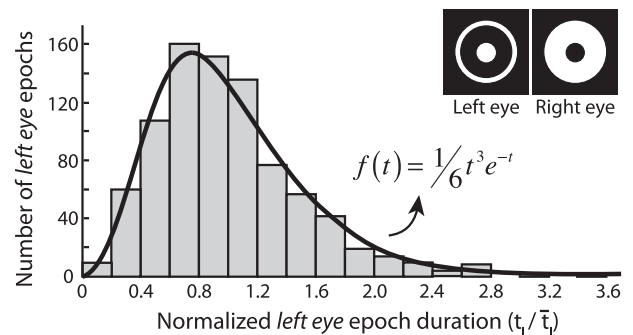


Fig. 2. Distribution of dominance times in binocular rivalry. The inset shows a stimulus pair used for inducing binocular rivalry. Observers pushed a response key as long as the black center disk was dominant. This resulted in the depicted normalized histogram of dominance durations. Also displayed is the best fitting density function. Image adapted from Levelt (1965).

in the equibrightness measurements. That result was indeed obtained. The left eye dominance durations decreased, again preserving Proposition II since the extra disk did not alter the average dominance duration of the white right eye center disk.

In addition to providing empirical support for the propositions, the records from the ten observers in these experiments were also used to study the statistics of the dominance duration (\bar{t}_i) distribution. For nine out of ten observers, the mean and standard deviation (σ) were related by $\bar{t}_i = 2\sigma_i$, which held for both small and large \bar{t}_i . The dominance duration distributions could be fitted by a gamma distribution (Eq. (2)).

$$f(t) = \lambda/3!(\lambda t)^3 e^{-\lambda t} \quad (2)$$

Here, λ is a scale factor. The normalized distribution (t_i/\bar{t}_i), eliminating λ , is plotted in Fig. 2. The exponent exp of t was derived, from the empirical $\bar{t}_i = 2\sigma_i$, as having the value 3. As possible interpretation of this integer exponent it was suggested that the suppressed stimulus generates a series of *excitation spikes*, each waiting time governed by $f(t) = \lambda e^{-\lambda t}$. The sum of waiting times for 4 such excitation spikes produces the observed gamma distribution, which means that in general the suppressed stimulus regains dominance after the fourth *spike*. The scale factor (λ) then denotes the stimulus strength (λ) of the recessive stimulus, as defined above. The average inter-spike time for these measurements was 650 ms. An intriguing question remained unanswered: could this concept of excitation spikes be given any neurophysiological interpretation? The question relates to the shape of the distribution of dominance durations, which will be further considered in Section 6.

4. Developments since 1965

The four propositions that Levelt formulated in 1965 still feature prominently in today's binocular rivalry literature. While this is an indication of their continued ability to capture many experimental findings, knowledge has certainly advanced since the propositions' original conception, and there are novel findings that suggest a critical evaluation of the propositions. In this section we will summarize current ideas about the role of stimulus strength in binocular rivalry, evaluating each of the propositions in the face of the developments of the last fifty years, and in several cases proposing modifications that capture these developments.

4.1. Stimulus strength

As detailed above, the stimulus parameters whose effects Levelt summarized using the concept of stimulus strength were the density, luminance contrast and blur of image contours. The former two scale positively with stimulus strength, the latter one scales negatively. Today, additional stimulus parameters whose effects on binocular rivalry appear to be captured by a general description in terms of stimulus strength, include color contrast (Bossink, Stalmeier, & De Weert, 1993), the motion content of a dynamic stimulus engaged in rivalry (Blake, Zimba, & Williams, 1985; Bossink et al., 1993; Platonov & Goossens, 2013; Wade, de Weert, & Swanston, 1984), and even stimulus onset asynchrony between eyes during intermittent stimulus presentation (van Boxtel, van Ee, & Erkelens, 2007). The established effect of stimulus blur, moreover, can likely be decomposed into two separate effects, one of spatial frequency content (Arnold, Grove, & Wallis, 2007; Baker & Graf, 2009a; Fahle, 1982; Wade et al., 1984) and one of contrast. The effect of absolute luminance has also been investigated but appears more variable (Fahle, 1982; O'Shea, Blake, & Wolfe, 1994).

It has been noted that stimulus properties associated with low stimulus strength are often properties that, outside of the lab, are typical of elements in our visual environment that are located

away from the plane of fixation. This suggests a relation between, on the one hand, experimental paradigms involving binocular rivalry and binocular brightness interaction and, on the other, the everyday occurrence of perceptual suppression when elements outside of the fixation plane are not matched between the retinas (Arnold et al., 2007; see also Arnold, 2011; Fahle, 1982; Leopold et al., 2005; O'Shea, 2011).

When we consider the progress that has been made in understanding the relation between stimulus strength and the phenomenology of binocular rivalry (and, also, other bistable phenomena), it is helpful to realize that several studies have addressed this relation using factorial designs. In such designs, rather than fixing the strength of one stimulus and varying the strength of the other, both stimuli's strengths are varied independently so that many combinations of the two stimulus strengths can be tested. As will be shown below, this has profound implications for how the results of such studies should be interpreted in the context of Levelt's original propositions, and it is one of the primary reasons that current knowledge is not always captured by the original four propositions, which were based on unilateral stimulus manipulations. We will further expand this notion in a discussion of each individual proposition.

4.2. Proposition I. Increasing stimulus strength for one eye will increase the perceptual predominance of that eye's stimulus

In the original context described above, where stimulus strength was understood to have a constraint in terms of binocular brightness interaction, this proposition helped to characterize the link between that phenomenon and binocular rivalry. Moreover, given the more specific original meaning of stimulus strength, in terms of contour density, contrast and blur, Proposition I originally helped characterize the influence of those physical parameters on binocular rivalry. In a modern context, where potential relations to binocular brightness interaction are often not considered and where the term 'stimulus strength' refers generally to a stimulus' potential to suppress another stimulus, Proposition I becomes a tautology, as it essentially reads 'increasing a stimulus' potential to suppress another stimulus increases the proportion of time it suppresses the other stimulus'. Nevertheless, the proposition has remained useful in recent times, as a tool for identifying stimulus properties that are associated with stimulus strength. Specifically, it is customary to designate any stimulus property whose value affects predominance during binocular rivalry, as a property that factors into stimulus strength. This then allows further manipulations of this property to be evaluated against the remaining propositions, which are phrased in terms of stimulus strength.

As will be reviewed below, this approach is valuable in practice, as it leads to coherent results in the vast majority of known cases. Specifically, if a given stimulus property is identified as affecting stimulus strength on the basis of Proposition I, then further evaluations in terms of the other (modified) propositions are generally consistent with this assessment. It should be noted, however, that, on a neural level, perceptual predominance is plausibly determined by a multitude of both interocular and intraocular factors, which are collapsed onto the single concept of stimulus strength when strictly defined in terms of Proposition I. It seems inevitable, therefore, that there are limits to stimulus strength as a unitary concept, and to this use of Proposition I. This concern may be especially pertinent for stimulus manipulations that impact relatively complex, mid- or high-level aspects of visual processing such as perceptual grouping or modulation by stimulus context (Albright & Stoner, 2002; Klink, Van Wezel, & Van Ee, 2012). In fact, one known stimulus property whose influence does not appear to be captured by the unitary concept of stimulus strength, is the

orientation uniformity of textures. Specifically, in rivalry between oriented textures, increasing the orientation jitter among the elements that form one eye's texture raises that eye's perceptual predominance (Bonneh & Sagi, 1999), so Proposition I suggests that orientation jitter scales positively with stimulus strength. This interpretation, however, leads to unexpected results when the effects of bilateral changes of orientation jitter are compared to Proposition IV (Bonneh, Sagi, & Karni, 2001). Manipulations of orientation uniformity, therefore, appear to call for more refined conceptualizations of stimulus strength, perhaps ones that are more closely related to the complex of neural factors that influence perceptual predominance. Although such conceptualizations may reveal important aspects of binocular rivalry that are not apparent when treating stimulus strength as a unitary concept, we reiterate that this simplified notion of stimulus strength does suffice to concisely describe the effects of the vast majority of known stimulus manipulations.

4.3. Proposition II. Increasing stimulus strength for one eye will only affect the average perceptual dominance duration of the other eye's stimulus

Proposition II is the most counterintuitive of the four, as it suggests that one cannot change a given eye's dominance durations by changing that eye's stimulus itself, but only by changing the other stimulus. Fig. 3A, left, schematically illustrates the observations in the original monograph that most clearly speak to this proposition (its Experiments 11 and 12, described in more detail above). While fixing the right eye's stimulus strength at a high level, these experiments systematically decreased the stimulus strength of the left eye to lower levels. As discussed above, this caused systematic changes in the right eye's mean dominance duration but not in the left eye's own mean dominance duration. Although stimulus strength of the right eye was kept fixed throughout these experiments, Fig. 3A, right, introduces an alternative representation of these data that provides room for visualizing many combinations of stimulus strength, such as might be probed using a factorial design that varies both strengths independently. As will become clear below, the ability to depict the full range of such combinations is useful when illustrating the relation between Levelt's original findings regarding Proposition II and more recent findings. In the new representation on the right, the x and y-axes denote the stimulus strengths of the two eyes, now labeled X and Y, and the z-axis shows the mean dominance duration of one eye, X in this case. By labeling the left eye either X or Y (and the right eye either Y or X) we can re-plot both curves from the left graph together in this representation. In addition, the meshed surface illustrates the overall relation between stimulus strength and dominance duration that is prescribed by Proposition II: one where the mean dominance duration of X only depends on the strength of Y.

Several later studies included conditions that resembled Levelt's original experiments in the respect that one eye's stimulus strength was fixed at a relatively high level while only the other eye's stimulus strength was varied (Blake, 1977; Bossink et al., 1993; Fox & Rasche, 1969; Leopold & Logothetis, 1996; Logothetis, Leopold, & Sheinberg, 1996; Mueller & Blake, 1989; Shiraishi, 1977). These studies invariably showed a large change in the mean dominance duration of the fixed-strength eye, consistent with Proposition II. However, some of these studies also reported a modest but significant change associated with the variable-strength eye (Bossink et al., 1993; Mueller and Blake, 1989; Shiraishi, 1977). This scenario is illustrated in the top left panel of Fig. 3B.

More recent experiments used factorial designs, applying a more varied set of stimulus strength combinations to investigate the predictions of Proposition II. Importantly, these experiments

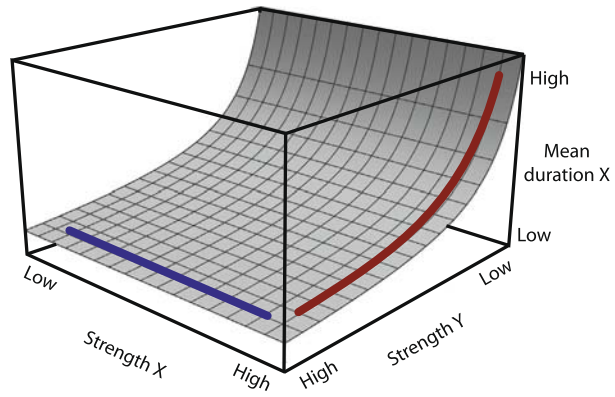
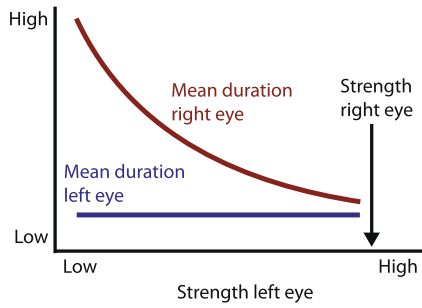
also included conditions where one eye's strength was fixed at a relatively low level while the other eye's strength was varied, a situation that, up until then, had not received much attention (Brascamp et al., 2006; Kang, 2009; Moreno-Bote et al., 2010; Platonov & Goossens, 2013). This approach revealed a markedly different pattern of results than what had been shown in the earlier work. Under these conditions, the largest change in dominance durations tended to occur for the variable-strength eye rather than the fixed-strength one (Fig. 3B, bottom left). The right panel of Fig. 3B re-plots all four curves of Fig. 3B, left, in the three-dimensional representation introduced above, and interpolates these findings to a surface that illustrates the overall suggested relation between stimulus strength and dominance duration. Note that the exact shape of this surface is an inessential feature of this illustration, but that the data do impose some degree of upward curvature as one moves from left to right in this figure. Specifically, the data of Fig. 3B's top left panel dictate a steeper slope of the surface along the solid red curve than along the solid blue curve, and the data of the bottom left panel pose an analogous constraint regarding the dashed curves. The resulting surface is consistent with the data from the earlier experiments and, within the range of stimulus strengths covered by those experiments, also with Proposition II. However, outside of this range it does not follow the proposition, but it shows the opposite pattern instead. Integrating the newer results with the older data, this recent work has led to the modified view that the largest change in percept durations tends to be associated with the eye that is presented with the strongest stimulus, regardless of which eye's stimulus strength is varied. In fact, with the benefit of hindsight it is apparent that several earlier studies already obtained data consistent with this modified view, but did not interpret those data as a general result (Fig. 1E in Bossink et al., 1993; Fig. 3 in Meng & Tong, 2004; Fig. 1C in Bonneh et al., 2004). One cautionary note, on which we will elaborate later, pertains to the relevance of stimulus size in this context (Kang, 2009).

The inset in the right panel of Fig. 3B uses the same space as its main plot, but illustrates the mean dominance durations of the other eye, marked Y. In both the inset and the main plot, the straight dashed line indicates the diagonal in 'stimulus-strength space' where the stimulus strengths for eyes X and Y are equal (relative to the surface in the main plot, the surface in the inset is simply mirrored in this diagonal). The addition of this inset provides another way of appreciating the rule formulated above: to the right of this diagonal, where X has a higher strength than Y, changes in the duration of X are larger than changes in the duration of Y, and to the left of the diagonal the opposite occurs.

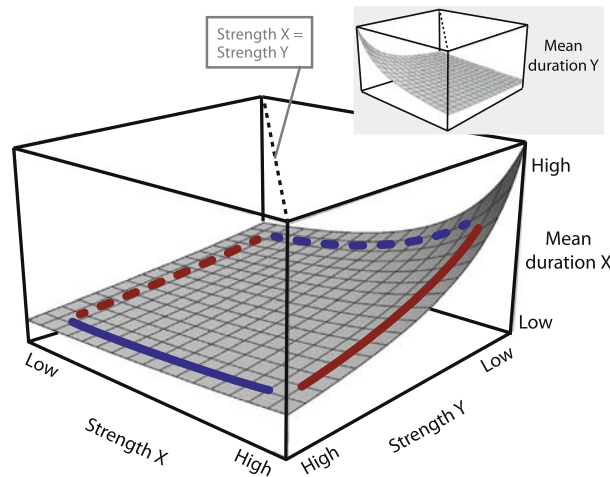
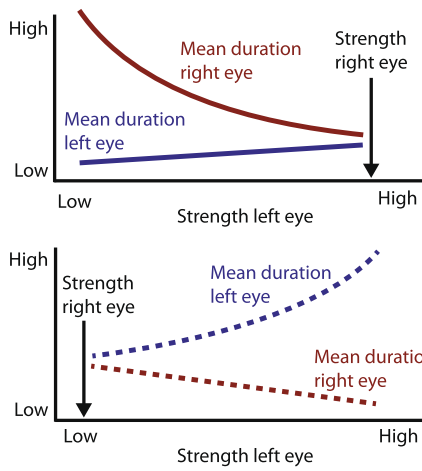
4.4. Proposition III. Increasing stimulus strength for one eye will increase the alternation rate

As has been pointed out before, Proposition III is closely related to Proposition II (e.g., Moreno-Bote et al., 2010). Indeed, the assessment of Proposition III is affected by the same findings that we discussed above in the context of Proposition II. Fig. 3C illustrates this. On the left side of this figure, where the right eye views a stronger stimulus than the left eye does, the primary effect of increasing the left eye's stimulus strength is to shorten the right eye's dominance durations while leaving the left eye's dominance durations largely unaffected. This is consistent with the original Proposition II, and the net result in terms of alternation rate, an increase, is consistent with the original Proposition III. On the right side of the figure, however, the left eye has the stronger of the two stimuli, so increasing the strength of the left eye's stimulus even further will primarily act to increase the left eye's own dominance durations, which is the opposite of what the original Proposition II predicts. Consequently, the net result in terms of alternation rate, a

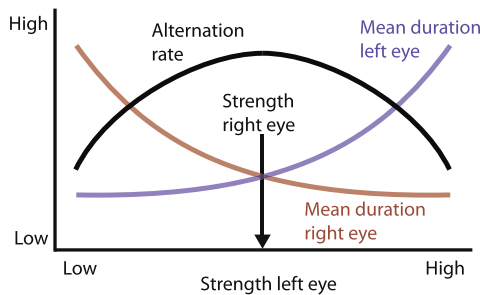
A. Proposition II: original findings



B. Proposition II: recent findings



C. Proposition III: recent findings



D. Proposition IV

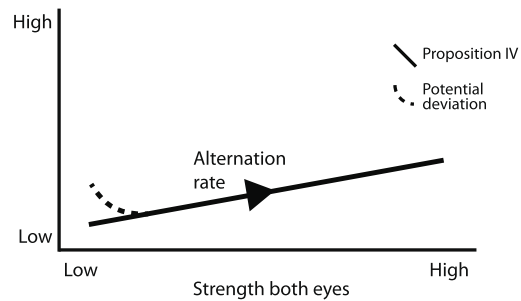


Fig. 3. Developments concerning Proposition II–IV. (A) Results of the 1965 experiments that confirmed Proposition II. If the stimulus strength in the left eye is decreased from being equal to that in the right eye to being much lower, this only affects the mean dominance duration of the right eye’s stimulus (red line), not that of the left eye’s stimulus (blue line). This basic effect (left panel) can be extrapolated to a surface (right panel) in stimulus-strength-space where strengths X and Y denote the strengths of the stimuli in the two eyes. (B) Later experiments found that decreasing the left eye’s stimulus does, in fact, also moderately change the dominance durations of the left eye’s stimulus (top left panel). They also showed that increasing the left eye’s stimulus strength from a situation where both eyes’ stimuli are weak, evokes the strongest effect on the left eye’s dominance durations while having only a small effect on the right eye’s dominance durations (bottom left panel). In the right panel these findings are displayed in stimulus-strength-space and interpolated to a surface that shows dominance durations of an eye labeled X. The dashed diagonal depicts the border where both stimuli are equally strong, and the inset shows the inverse surface for the durations of the other eye, Y. These surfaces illustrate that any increase in the stimulus strength difference between the two eyes (i.e. any movement away from the dashed diagonal) primarily leads to an increase in the average perceptual dominance duration of the strongest stimulus. (C) Depiction of how Proposition III is related to Proposition II. On the left side of the arrow that denotes equal stimulus strengths for the left and right eye, the original Propositions II and III hold. Increasing the left eye’s stimulus strength mainly decreases the right eye’s dominance durations, causing an increase in alternation rate. On the right side of the arrow the opposite holds true: when the left eye’s stimulus strength is increased beyond being equal to the right eye’s stimulus strength, the main effect is an increase in the left eye’s dominance durations and, consequently, a decrease in alternation rate. In other words, manipulations that increase the stimulus strength difference between the two eyes, reduce the perceptual alternation rate. (D) Proposition IV predicts an increase in alternation rate when both eyes’ stimuli are increased in strength. This effect, although moderate, is generally found, but computational models predict a deviation from this relation at very low stimulus strengths (dashed line).

reduction, is also the opposite of what the original Proposition III predicts. Given that the transition between these two scenarios tends to lie near the point where both eyes’ stimuli have equal strengths, the rate of perceptual alternations should peak around

that same point, and this is indeed what has been found (Moreno-Bote et al., 2010). Note that this inference does not rely on the exact choice of curve shapes in Fig. 3C, as long as the curves comply with the findings described in Section 4.3; i.e. as long as the

red curve runs more steeply than the blue curve on the left side of Fig. 3C, and the blue curve runs more steeply on the right side. One way to concisely summarize these findings is by stating that any manipulation that increases the difference between the two eyes' stimulus strengths will reduce the perceptual alternation rate.

4.5. Proposition IV. Increasing stimulus strength in both eyes while keeping it equal between eyes will increase the perceptual alternation rate

Changes in stimulus strength tend to affect perceptual dominance durations more when applied differentially to the two eyes than when keeping both eyes matched (Brascamp et al., 2006; Moreno-Bote et al., 2010). Experiments testing Proposition IV, therefore, generally have to rely on relatively modest changes in percept duration. Nevertheless, many studies have provided data in support of Proposition IV (Bonneh, Sagi, & Karni, 2001; Hollins, 1980 for stimulus contrast; Brascamp et al., 2006; Buckthought et al., 2008; Kang, 2009; Meng & Tong, 2004; Platonov & Goossens, 2013; van Ee, 2009), and the generality of the proposition was not doubted until recently.

The recent development that did spark some discussion, was the finding that a large class of computational models that otherwise describe rivalry dynamics fairly well, predict a deviation from Proposition IV (Curtu et al., 2008; Seely & Chow, 2011; Shpiro et al., 2007). In particular, whereas the proposition describes a positive relation between stimulus strength and alternation rate (Fig. 3D, solid line), these models predict that this relation should reverse at very low levels of stimulus strength (Fig. 3D, dashed line). Although such model behavior is not absolutely inevitable (Ashwin & Lavric, 2010; Kilpatrick & Bressloff, 2010; Moreno-Bote, Rinzel, & Rubin, 2007; Seely & Chow, 2011), its appearance for a wide range of plausible model implementations seems sufficient reason for closer empirical examination.

To date, one study has specifically searched for the predicted deviation, and surprisingly obtained support for both the original proposition and the predicted deviation (Platonov & Goossens, 2013). Specifically, data were consistent with Proposition IV when the authors manipulated stimulus strength using the conventional parameter of luminance contrast, but showed the predicted deviation when the stimulus' motion content was adjusted to control stimulus strength, instead. As discussed later, there appears to be a plausible explanation for this difference (Platonov & Goossens, 2013; Seely & Chow, 2011), but the issue certainly warrants further investigation.

Finally, we briefly reiterate the case of rivalry between oriented textures (Bonneh, Sagi, & Karni, 2001). As discussed at the end of Section 4.2, we tentatively interpret the apparent violation of Proposition IV that arises when varying the orientation coherence of these textures, not as a shortcoming of Proposition IV, but as illustrative of the notion that stimulus strength as a unitary concept may not suffice to capture effects of higher-level stimulus manipulations.

4.6. Modified propositions

The long-lasting influence of Levelt's (1965) approach derives, in part, from the practical value of summarizing a diverse set of observations in a small number of propositions that can be applied and tested experimentally. At the same time, the developments described above indicate that the original propositions no longer fully capture existing evidence. We will therefore attempt to formulate a modified set of propositions, derived from the original propositions but reflecting present-day knowledge.

- I. Increasing stimulus strength for one eye will increase the perceptual predominance of that eye's stimulus.
- II. Increasing the difference in stimulus strength between the two eyes will primarily act to increase the average perceptual dominance duration of the stronger stimulus.
- III. Increasing the difference in stimulus strength between the two eyes will reduce the perceptual alternation rate.
- IV. Increasing stimulus strength in both eyes while keeping it equal between eyes will generally increase the perceptual alternation rate, but this effect may reverse at near-threshold stimulus strengths.

There is an intentional one-to-one correspondence between these four Modified propositions and the original ones. Whereas this makes explicit the historical origins of the Modified propositions, it does introduce some redundancy. Specifically, as mentioned above, the modern rendition of Proposition I is essentially a tautology, and Modified Proposition III is an inescapable consequence of Modified Proposition II. Since Modified Propositions II and IV are thus the only two uniquely informative propositions they might be regarded as the two 'core laws of binocular rivalry'.

4.7. Mixed dominance and stimulus size

Given the rich diversity of experimental findings in this field, almost any general rule will come with caveats, and so do the Modified propositions we just formulated. This is already clear from our use of the word 'may' in Modified Proposition IV, but there are additional caveats, concerning mixed dominance and stimulus size. The above analyses have implicitly assumed that, at any given time during binocular rivalry, either of the eyes' stimuli is perceived exclusively. In reality, some proportion of the time is taken up by perception of a composite of both stimuli (Yang, Rose, & Blake, 1992). These periods of mixed perception have their own interesting dependence on stimulus parameters (Brascamp et al., 2006; Hollins, 1980; Kang et al., 2010; Knapen, van Ee, & Blake, 2007; Mueller & Blake, 1989; O'Shea, Sims, & Govan, 1997) and on stimulation history (Hollins & Hudnell, 1980; Klink et al., 2010; Said & Heeger, 2013; Wolfe, 1983). It is also clear that the characteristics of these mixed periods are to some extent interrelated with the perceptual dominance durations that are the topic of this study (Kang et al., 2009), although more research is needed. For the purposes of our present discussion, two observations regarding periods of mixed dominance are critical.

First, the contribution of mixed percepts during binocular rivalry increases with the retinal size of the stimulus, with larger stimuli tending to give rise to more 'piecemeal dominance': simultaneous perception of parts of both stimuli in complementary regions of the visual field (Blake, O'Shea, & Mueller, 1992; O'Shea, Sims, & Govan, 1997). This is consistent with the idea that rivalry is resolved more or less independently per local retinal region (Blake, O'Shea, & Mueller, 1992; Kovács et al., 1996; Lee, Blake, & Heeger, 2007; Wilson, Blake, & Lee, 2001). Interestingly, whereas the rule presented as Modified Proposition II is based on data from relatively small stimuli, Kang (2009) observed that behavior more like the original Proposition II can emerge when using larger stimuli, thus allowing more piecemeal dominance (i.e. behavior like the surface in the right panel of Fig. 3A). We will treat the behavior described by the Modified Proposition II (and the associated Modified Proposition III) as the general result, in part because this will enable us to demonstrate close parallels with observations from other bistable perceptual phenomena. Nevertheless, it is remarkable that changes in stimulus size, or global configuration, can apparently bridge the gap between the two patterns of behavior. The reasons for this are not fully understood, but simulation work in Kang (2009) provides some indications, and we will

discuss another perspective on the issue in a later section (final paragraphs of Section 7.3).

Mixed perception during binocular rivalry is also relevant to the discussion of Proposition IV and its potential limitation at low stimulus strengths predicted by Shpiro et al. (2007). Conditions where this limitation would become apparent, are typically also conditions where a different kind of mixed perception, termed superimposition, tends to be prevalent (Brascamp et al., 2006; Hollins, 1980; Liu, Tyler, & Schor, 1992; van Ee, 2009). This means that alternation rate, the variable central to Proposition IV, cannot be calculated from exclusive dominance durations alone, as mixed phases should be factored in as well (expressed in the terms used in the section about the 1965 context, the equality $\bar{T} = \bar{t}_l + \bar{t}_r$ no longer holds). The comparison of empirical data with results from models that predict these limitations of Proposition IV is further complicated by the fact that these models tend not to display any behavior that might correspond to superimposition under the relevant conditions (Seely & Chow, 2011).

5. Validity of the propositions beyond binocular rivalry

An interesting development in recent years has been the accumulation of evidence that many of the above results generalize to bistable perceptual phenomena that might otherwise appear quite different from binocular rivalry. We will discuss this development here, dividing the relevant studies into two categories. The first category consists of studies that systematically varied a single physical stimulus property between one extreme where it favored one percept, and another extreme where it favored the other percept. The schematic illustration of Fig. 3C is an example of such a scenario, and shows the type of outcome that would be expected according to the Modified Propositions. In the second category

are studies that systematically and independently varied the strengths of both stimuli involved, thus making for a factorial design. The exact predictions for such designs will be discussed before presenting the data from those studies.

For convenience, our visualizations of the empirical data will focus on alternation rate rather than percept durations, and therefore on Modified Proposition III. There is always, however, a direct relation to percept durations and Modified Proposition II, as should be clear from Fig. 3C. Furthermore, our visualizations will follow Moreno-Bote et al. (2010) in plotting alternation rate as a function of the predominance of a given percept, rather than plotting it as a function of the physical stimulus parameter that was modulated (e.g. contrast). In other words, even though the independent variable is always a stimulus property, this approach does not explicitly depict the values of this independent variable but plots the resulting values of two dependent variables against each other (predominance and alternation rate). As will become clear below, this approach has the distinct benefit of allowing a comparison to bistable phenomena for which perceptual predominance can be varied but for which no physical parameter indexes the strength of one of two competing stimuli in a straightforward fashion (Moreno-Bote et al., 2010). The approach, furthermore, is a natural extension of the common (albeit somewhat circular) operational interpretation of Proposition I discussed above, which holds that strong stimuli are ones that have a high perceptual predominance, so that perceptual predominance can act as a proxy for stimulus strength itself.

5.1. Category I. Experiments that varied a single parameter

5.1.1. Bistable depth ordering of ambiguous plaids

Two grating patterns that are superimposed and that move in different directions behind an aperture (Fig. 4A, left panel) create

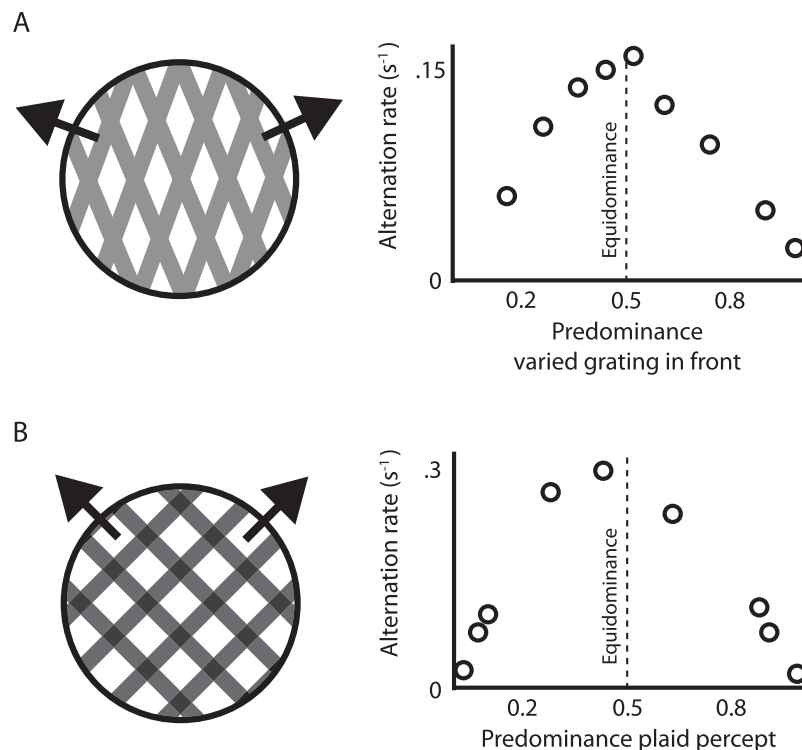


Fig. 4. Two bistable phenomena other than binocular rivalry that show compliance with the Modified Propositions. (A) Two superimposed grating that move in different directions behind an aperture (left) create a depth ordering ambiguity for which the perceptual predominance can be modulated by changing the wavelength (spatial frequency) of one of the gratings. When the predominance is plotted against the alternation rate (right; Moreno-Bote et al., 2010; their Fig. 8) a pattern arises that peaks at the point of equidominance, consistent with Modified Proposition III. (B) Changing the angle between two superimposed moving gratings (left) affects the predominance of perceiving a coherent plaid pattern rather than two individual gratings. The relation between predominance and alternation rate (right; Moreno-Bote et al., 2010, their Fig. 8) again peaks at the point of equidominance.

a bistability in their perceived depth ordering. Each grating is perceived to be in front for brief periods at a time, and perception alternates between the two configurations. Moreno-Bote and colleagues explored the stimulus parameters that affect the balance between the two perceptual interpretations (Moreno-Bote et al., 2007), and later extended this work by systematically varying one of these parameters, the wavelength of one of the gratings, over a large range (Moreno-Bote et al., 2010). The effect of this manipulation is re-plotted from the original paper in Fig. 4A (right panel), with the x-axis showing the perceptual predominance of the configuration in which the varied grating is in front, and the y-axis showing the associated alternation rate. Following the same reasoning outlined above, the x-axis point where perceptual predominance of both depth ordering interpretations is 50% corresponds to a situation where the stimulus strengths of both gratings are equal: the point of *equidominance* (in this particular case, this is close to the point where both gratings have the same wavelength). Thus, the figure shows that modifying the wavelength of one of the gratings increases the perceptual alternation rate up to the point where both gratings have the same stimulus strength, and reduces the alternation rate beyond that point. In other words, any change that increases the difference between two gratings' stimulus strengths, causes the alternation rate to go down. This indicates that ambiguous depth ordering, like binocular rivalry, complies with Modified Proposition III and, by inference, also with Modified Proposition II (compare with Fig. 3C).

Moreno-Bote et al. (2010) furthermore observed that the data pattern of Fig. 4A is close to symmetrical around the point of equidominance, and that the same can be said of data from other stimuli they tested. This near-symmetry has interesting implications for the interpretation of the results in terms of neural mechanisms, as we will later discuss.

5.1.2. Bistable motion of ambiguous plaids

Of all bistable phenomena outside of binocular rivalry to be systematically studied with Levelt's propositions in mind, moving plaid ambiguity appears to have been the first. The stimulus again consists of two superimposed grating patterns translating behind an aperture (Fig. 4B, left panel). However, this stimulus is modified in a way that gives rise to a different kind of bistability in which the two gratings are alternately perceived as forming a rigid plaid that moves coherently in one direction, or as two separate gratings sliding in different directions (Wallach, 1976).

Hupé and Rubin (2002, 2003) and Rubin and Hupé (2005) investigated the dynamics of alternations between these two percepts. Among several other contributions, they explored the stimulus manipulations that influence these dynamics, and compared the effects of one of these manipulations to Levelt's original Proposition II. More recently Moreno-Bote et al. (2010) built on these findings by systematically varying the angle between the two gratings from values that favor perception of a single plaid to values that favor perception of two separate gratings. Note that this is a case where there exists no clear relation between the physical parameter that is varied (angle) and the strength of either particular stimulus, as both gratings whose mutual angle is varied are represented in both percepts, and varying the angle plausibly affects the potency of both these percepts simultaneously. This is when the benefit of the visualization method adopted in Fig. 4A becomes clear, as one can still plot alternation rate as a function of perceptual predominance (Fig. 4B, right panel), and observe that alternation rate again peaks near the point of equidominance. This demonstrates consistency with Modified Proposition III and, by inference, Modified Proposition II, for this form of bistable perception.

5.2. Category II. Factorial designs

Other bistable perceptual phenomena for which compliance with Levelt's propositions has been investigated, were all studied using factorial experimental designs. Before discussing those phenomena we will first detail the predictions for factorial designs that follow from what has been discussed so far. These predictions have not been explicitly identified elsewhere, but they follow directly from the combination of Modified Proposition III and (Modified) Proposition IV, and they will be helpful in interpreting results from factorial designs. The reasoning behind these predictions is illustrated in Fig. 5A. Given that the predictions pertain to many different combinations of the two stimulus strengths, this figure takes inspiration from the three-dimensional visualization that we used in Fig. 3A and B, which allows convenient illustration of many such combinations. Specifically, the plots shown in the top row of Fig. 5A depict top views of the three-dimensional space that was shown in Fig. 3A and B, with each axis depicting one of the two stimulus strengths and with the arrows indicating various stimulus strength manipulations. The bottom row of plots in Fig. 5A, in turn, depicts the patterns of alternation rates that are predicted to result from the manipulations shown in the top row. Following this organization, the left column of plots in Fig. 5A shows that Modified Proposition III describes a change in stimulus strength for only one of the eyes and that the result is an alternation rate that peaks near the point where both strengths are equal (dashed line; bottom; cf. Fig. 4A). In an analogous fashion, the middle column of plots describes (Modified) Proposition IV (not including the potential limitation that may apply at extremely low stimulus strengths). The right column then illustrates a prediction for factorial designs that inevitably follows from combining these two propositions. Specifically, when keeping one stimulus' strength fixed, changing the other strength (indicated by a shaded arrow) will cause alternation rate to reach its peak near the point where both stimulus strengths have the same level, but the precise height of this peak will depend on what that level is.

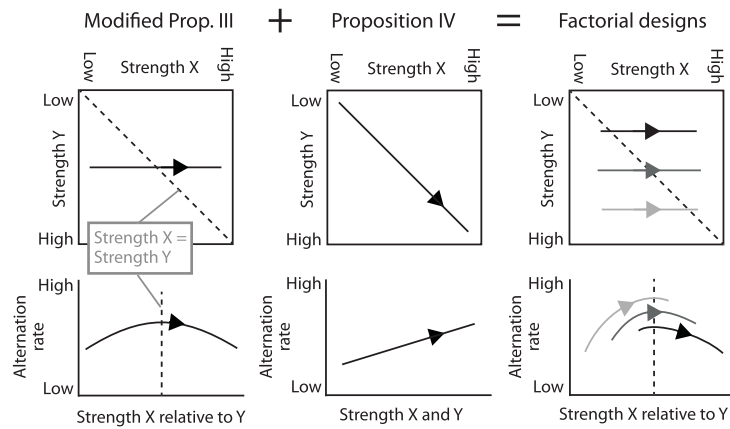
For illustration, Fig. 5B uses this same format to re-plot the results of a factorial experiment involving binocular rivalry (Brascamp et al., 2006). Each shade corresponds to a situation where stimulus contrast was kept fixed for eye Y, and each marker of that shade corresponds to a different stimulus contrast presented to eye X. The results are as described above, indicating agreement with Modified Propositions III and IV (and, by inference, also with Modified Proposition II).

5.2.1. Bistable structure-from-motion

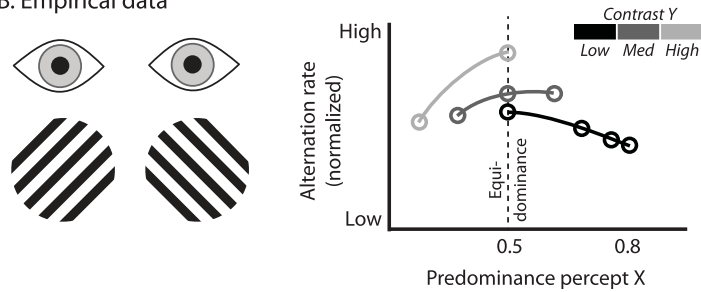
When viewing a flat projection of a three-dimensional object, one cue that still allows a three-dimensional structure to be perceived is object motion (Wallach & O'Connell, 1953). In some cases, however, there are two plausible moving objects that both correspond to the same two-dimensional projected pattern of motion, a situation that prompts so-called bistable structure-from-motion. One popular example involves a transparent sphere with a dotted surface, revolving around a vertical axis that is parallel to the projection plane. While viewing a projection of such a sphere (Fig. 5C, left panel) elicits vivid perception of a rotating three-dimensional sphere, the direction of rotation is ambiguous and perceived rotation reverses at irregular intervals. Sometimes the leftward-moving dots appear to be forming the sphere's front surface; sometimes they appear to be forming the sphere's back surface.

Brouwer and van Ee (2006) observed that the rate of alternations between these percepts rose when either the density or the speed of the dots was increased. If we take these manipulations to entail increases in stimulus strength, then this is consistent with (Modified) Proposition IV. More recently, Klink, Van Ee, and Van Wezel (2008) used a factorial design to independently vary the

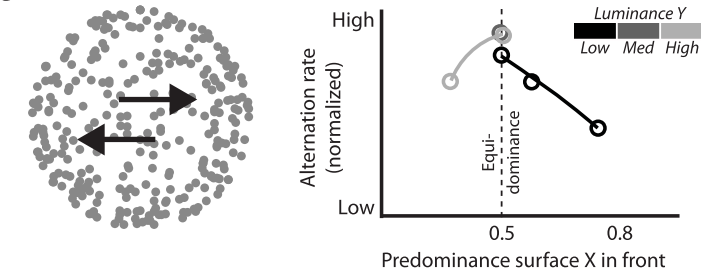
A. Prediction based on Modified Propositions III and IV



B. Empirical data



C



D

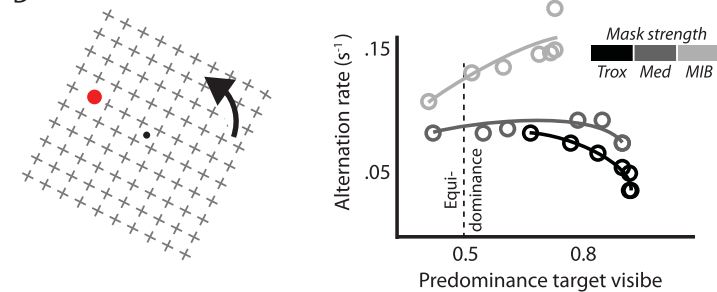


Fig. 5. Additional bistable phenomena, and their compliance with Modified Propositions III and IV. (A) When Modified Proposition III and IV are combined they predict that, in factorial designs, the alternation rate always peaks near the point of equidominance, but that the height of this peak will depend on the stimulus strengths that are used. (B) Re-plotted data from a binocular rivalry experiment (Brascamp et al., 2006; their Fig. 3) confirms the predictions in (A). (C) Re-plotted data from an experiment with bistable structure-from-motion (left panel; Klink, Van Ee, & Van Wezel, 2008; their Fig. 4A) also matches the predictions in (A). (D) Re-plotted data from a motion-induced-blindness experiment (Bonneh et al., 2014; their Fig. 3, right column) shows quantitative differences but qualitative similarities with the predictions in (A). See main text for more details. To avoid clutter throughout Fig. 5, the original data were re-plotted with the following caveats. Panels (B) and (C) show only data points that correspond to unique pairs of physical stimulus values (e.g. pairs of left-eye contrast and right-eye contrast), which means that we omitted data from a value pair a,b if the plot already depicts the data corresponding to the mirror pair b,a. For a three-by-three factorial design such as that of panel (C) this means that we show six (3!) rather than nine (3²) data points. Again for clarity, panel (B) omits the data from one of the four sampled contrast levels of Y (the second-lowest level), but those data are consistent with the depicted pattern. Similarly, panel (D) shows only three of the four mask strength levels sampled by Bonneh et al. (2014), omitting data from the static mask condition. Again, those data do conform to the overall pattern.

luminance of the leftward-moving dots and that of the rightward-moving dots. Consistent with earlier demonstrations (Doshier, Sperling, & Wurst, 1986; Schwartz & Sperling, 1983), this

manipulation influenced the balance between the two percepts, such that observers tended to see the higher-luminance dots in front. Fig. 5C (right panel), shows the results in the format

introduced above. Alternation rate peaks near the point of equidominance for each curve, but the level at which the equidominance line (dashed) is crossed differs between curves in the predicted fashion. As can be verified by a comparison to Fig. 5A, therefore, these results are consistent with the conclusions of Klink and colleagues that Modified Propositions III and IV (and, thus, also II) apply to bistable structure-from-motion as they do to binocular rivalry.

5.2.2. Motion-induced blindness

Motion-induced blindness (MIB) is a compelling form of perceptual bistability that was discovered relatively recently (Bonneh, Cooperman, & Sagi, 2001). Here an, in principle, salient stimulus (the target) is presented some distance away from fixation while a large pattern (the mask) moves within the visual field, encompassing the location of the target (but never occluding the target; Fig. 5D, left panel). This configuration causes the target to perceptually disappear and reappear at irregular intervals. To facilitate a comparison with other bistable phenomena, it is useful to think of MIB as a form of perceptual bistability where the ‘target visible’ percept involves perceptual dominance of the target, and the ‘target invisible’ percept involves perceptual dominance of the mask (Bonneh et al., 2014).

Several studies have addressed the influence of stimulus manipulations on the balance between the two perceptual states during MIB (Bonneh, Cooperman, & Sagi, 2001; Carter & Pettigrew, 2003; Graf, Adams, & Lages, 2002; Wallis & Arnold, 2008) and one includes a comparison with Levelt’s original Proposition II (Carter & Pettigrew, 2003). More recently, Bonneh et al. (2014) took a systematic approach, using a factorial design in which the strength of the target and that of the mask were varied independently. The strength of the target was manipulated by varying its luminance contrast. Mask strength, in turn, varied from ‘high’ for a fast-moving mask typical of the MIB paradigm, to ‘minimal’ in a condition where the mask was omitted altogether. Perceptual disappearances in this latter condition, in fact, would not typically be characterized as MIB but as Troxler’s fading (spontaneous perceptual disappearance of a peripheral target; Troxler, 1804). Bonneh and colleagues also included intermediate conditions where the mask was present but where it moved as a lower speed, with the objective of reducing its strength.

Fig. 5D (right panel), re-plots the results of Bonneh et al. (2014) in the same format as used above. Each shade corresponds to a situation where the strength of the mask was kept constant, and each plot marker in that shade corresponds to a different target luminance contrast. One clear conclusion comes from the lightest markers, which correspond to high mask strengths, the typical situation for MIB. For this mask strength the alternation rate keeps rising, even well to the right of the point where the target is visible 50% of the time. If we tentatively identify this as the point of equidominance, then this result violates Modified Proposition III, which predicts alternation rate to peak near equidominance. As Bonneh and colleagues note, this result is more consistent with Levelt’s original Propositions III and II than with the modified ones.

To gain a better understanding of this result it is useful not to assess the data of the high-strength mask (MIB) in isolation, but to consider all three curves of Fig. 3D together. It then becomes clear that these data bear a strong resemblance to those of other bistable perceptual phenomena. In particular, the vertical ordering of the three curves indicates compliance with Proposition IV (compare to Fig. 5A). Moreover, even though the alternation rate does not peak near 50% visibility, it does not monotonically rise either, with the intermediate mask strength yielding a peak near 80% visibility and the minimal mask strength (Troxler’s fading) resulting in a monotonically falling curve that is quite similar to the analogous curves for the other paradigms (black curves in Fig. 5B and C). In

other words, these analyses identify an overall correspondence between the phenomenology elicited by this stimulus and that observed in other forms of perceptual bistability, and the differences in stimulus-strength dependence seem of degree rather than kind. Potential reasons behind these differences will be discussed later in the context of underlying neural mechanisms.

5.3. Conclusion regarding the propositions’ validity beyond binocular rivalry

There is a large degree of similarity between the dynamics of various forms of bistable perception, regardless of whether the bistability arises from interocular conflict, depth ordering ambiguity, or other sources. For all forms of perceptual bistability discussed above there is broad agreement with the Modified Propositions, with various experiments showing behavior resembling Modified Propositions II/III (bistable structure-from-motion, MIB/Troxler’s fading) and (Modified) Proposition IV (bistable depth ordering of ambiguous plaids, bistable motion of ambiguous plaids, bistable structure-from-motion, MIB/Troxler’s fading). This similarity across paradigms can be easily overlooked when focusing on isolated aspects of the data (e.g. alternation rate does not generally peak near equidominance for MIB/Troxler’s fading; the effect of varying dot luminance for one dot direction in bistable structure-from-motion depends greatly on the luminance of dots moving in the opposite direction). The underlying similarity, however, becomes clearly apparent whenever one considers the overall data pattern arising from a sufficiently diverse set of stimulus strengths.

6. A note on the distribution of dominance times

Levelt’s (1965) monograph brought a second lasting contribution to the field of binocular rivalry research, besides the four propositions. This was the description of the statistical properties of the distribution of dominance durations. As it turns out, the way in which percept durations vary within a single condition is rather common across many perceptual bistability paradigms. Levelt characterized this variability for binocular rivalry by demonstrating that an observer’s percept durations in a given experimental session follow a right-skewed distribution that resembles a gamma distribution (Levelt, 1965). He additionally hypothesized that this might imply that the duration of dominance periods in binocular rivalry is governed by a discrete number of ‘excitation spikes’ of a stochastic process in the brain. More specifically, if such ‘spikes’ are generated by a Poisson process, then one would expect percept durations to follow a gamma distribution and to lack sequential correlation.

Nowadays, the finding that perceptual dominance durations follow a right-skewed distribution has been replicated for a broad range visual bistability paradigms, as has the finding that these durations show little sequential correlation (Borsellino et al., 1972; Brascamp et al., 2005; Carter & Pettigrew, 2003; De Marco, Penengo, & Trabucco, 1977; Fox & Herrmann, 1967; Holcombe & Seizova-Cajic, 2008; Murata et al., 2003; O’Shea et al., 2009; Pastukhov & Braun, 2011; van Ee, 2005, 2009; Walker, 1975). The notion that bistable perception shows no sequential dependence at all, however, has been drawn into question by recent work showing modest but consistent dependencies (Pastukhov & Braun, 2011; van Ee, 2009). Similarly, while the fitted distribution is in many cases indeed a gamma distribution (Kovács et al., 1996; Leopold & Logothetis, 1996; Logothetis et al., 1996; Murata et al., 2003; O’Shea et al., 2009; van Ee et al., 2006), other theoretical distributions have been used and appear comparably suitable (Brascamp et al., 2005; Lehky, 1995; Moreno-Bote et al., 2007; Shpiro et al., 2009; Zhou et al., 2004). These might be reasons

why attempts to further examine percept durations in terms of an underlying Poisson-like process have been fairly limited (Blake, Fox, & McIntyre, 1971; Murata et al., 2004, 2003).

The shape of the dominance time distribution has, however, been a recurring topic of interest. It has been shown to be rather similar for humans and non-human primates (Leopold & Logothetis, 1996) and together with the degree of serial correlation between dominance times it has been an important element in the debate on the relative roles of neural adaptation and neural noise in driving perceptual alternations (Fox & Herrmann, 1967; Moreno-Bote et al., 2007; Pastukhov et al., 2013; Shpiro et al., 2009; van Ee, 2009). On a general level, the distribution's peaked, rather than monotonically decreasing, shape indicates that the probability of a perceptual switch is low during the time period immediately following the previous switch, a temporary stability that may reflect a lack of accumulated adaptation or some other stabilizing mechanism (Kloosterman et al., 2014; Moreno-Bote et al., 2007; Pastukhov et al., 2013). In addition, while dominance time distributions can be quite variable between individual observers, they do correlate within observers from one paradigm to the next (Carter & Pettigrew, 2003; Shannon et al., 2011; Sheppard & Pettigrew, 2006; see also Baker & Graf, 2009b; but see Gallagher & Arnold, 2014), which is consistent with the recent identification of genetic (Shannon et al., 2011) and neurochemical factors (van Loon et al., 2013) that influence dominance durations across paradigms.

7. Implications of the (Modified) propositions for neural mechanisms

Given the general applicability of our Modified propositions across many experimental situations, it is important to ask what the data patterns they describe could reveal about the underlying neural system. Some of the most explicit answers to this question are in terms of computational models that have been developed, often using these same data patterns as constraints, to formalize the brain's operations during binocular rivalry (incidentally, Levelt's (1965) monograph includes one of the first attempts at formalizing these operations in a schema in its Fig. 16 and associated text). The range of formal approaches to binocular rivalry in the literature is quite diverse (Blake, 1989; Borisjuk, Chik, & Kazanovich, 2009; Curtu et al., 2008; Gigante et al., 2009; Grossberg, 1987; Grossberg et al., 2008; Hohwy, Roepstorff, & Friston, 2008; Kalarickal & Marshall, 2000; Laing and Chow, 2002; Lehky, 1988; Moreno-Bote et al., 2007, 2010; Mueller, 1990; Noest et al., 2007; Noest & van Wezel, 2012; Said & Heeger, 2013; Seely & Chow, 2011; Shpiro et al., 2009; Stollenwerk & Bode, 2003; Sundaeswara & Schrater, 2008; Wilson, 2003, 2007). Nevertheless, certain commonalities can be identified across many models that display aspects of the behavior reviewed above. These common assumptions can be summarized as: (1) perception of each of the interpretations corresponds to high activity of a different neural population; (2) these populations either directly or indirectly inhibit each other; (3) either the populations themselves and/or their inhibitory connections gradually reduce their efficacy (i.e. adapt) during periods of high activity; (4) these populations' activities are subject to random fluctuations. At the broadest level, therefore, Levelt's propositions and related findings are consistent with the idea that this set of assumptions has merit, as is also suggested by other evidence (e.g. Alais et al., 2010; Blake, Sobel, & Gilroy, 2003; Kang & Blake, 2010; Lankheet, 2006; Pastukhov & Braun, 2011; Suzuki & Grabowecky, 2002; van Loon et al., 2013).

In some cases, analysis of these models leads to more specific inferences that, although inspired by specific models, apply to a relatively broad range of conceptualizations. These inferences will be reviewed next.

7.1. Modified propositions II and III

In its original form, stating that a change in one eye's stimulus strength only affects the other eye's dominance durations, Proposition II has sometimes been interpreted as a direct indication that binocular rivalry entails inhibitory interactions between two neural entities that correspond to the two percepts (e.g. Rubin & Hupé, 2005). Indeed, it seems intuitively clear how such a contralateral effect may arise if a change in stimulus strength affects the amount of inhibition brought about by the altered stimulus. In this sense, Modified Proposition II is still consistent with the notion of mutual inhibition, because it still describes the effect of a change in stimulus strength to be partly (although not exclusively) contralateral.

Modified Proposition II states that unilateral changes in stimulus strength primarily affect dominance durations of the eye with the stronger stimulus, and Modified Proposition III makes an equivalent statement in terms of alternation rate. An analysis by Wilson (2007) suggests why binocular rivalry may have this property. His model of binocular rivalry is of the general class described above, and in this model an alternation in perceptual dominance occurs when adaptation of the suppressed neural population decays (after having accumulated during perceptual dominance) to a critical level where the balance tips in favor of the currently suppressed population. The key observation here is that the decay of adaptation follows a decelerating curve: the initial drop in adaptation after the onset of suppression is relatively fast, but further decay then takes longer as adaptation approaches some minimal level. In the Wilson model, as in other models in this class, changes in either stimulus' strength can affect the critical level that the decaying adaptation must reach to trigger a perceptual switch. However, any given shift in the critical adaptation level has a larger effect on percept durations that are already long, because these involve a relatively shallow part of the adaptation decay curve (Fig. 6A). In contrast, during brief dominance periods adaptation drops quickly so dominance time depends relatively little on the precise distance adaptation has to drop (Fig. 6A), thus suggesting an explanation for the fact that stimulus changes generally have a relatively weak effect on the (already brief) dominance durations of a weaker stimulus.

The effect described above is not specific to the particular model used by Wilson (2007). Indeed, Laing and Chow's (2002) analysis of a different model points to a similar conclusion. One may conceive of dynamical systems where a different non-linearity than the described deceleration, for instance a non-linearity in the relation between stimulus strength and the critical level, augments or counteracts the effect described above. Nevertheless, we conclude that if the occurrence of a perceptual alternation depends on a decelerating progression toward a critical level, then this will introduce a tendency to comply with Modified Propositions II and III. We therefore see these propositions as consistent with the notion that binocular rivalry alternations depend on a form of adaptation. Note that the above line of reasoning stays essentially unaltered if the role of adaptation is not to make the system actually reach a critical point, but to bring the system gradually closer to a critical point so that random fluctuations become more likely to provide a final push (Brascamp et al., 2006; Huguet, Rinzel, & Hupé, 2014; Kang & Blake, 2011; Kim, Grabowecky, & Suzuki, 2006; Moreno-Bote et al., 2007; Pastukhov et al., 2013; Shpiro et al., 2009).

7.2. Proposition IV

The recent discovery that many models of binocular rivalry predict a deviation from the original Proposition IV in certain situations (Shpiro et al., 2007) has prompted relatively detailed

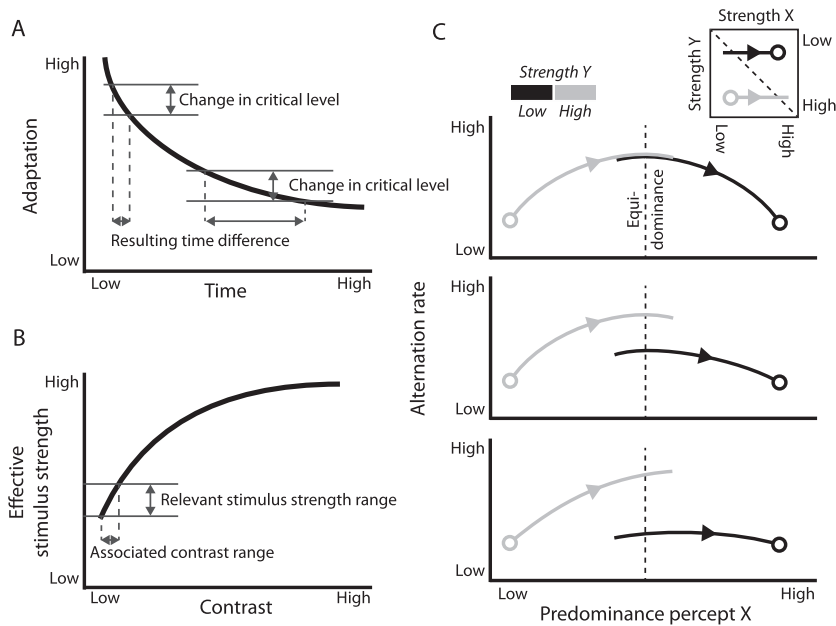


Fig. 6. Inferences regarding neural mechanisms. (A) Illustration of a potential explanation of Modified Proposition II in terms of neural adaptation. In a system in which perceptual switches are caused by a decelerating decay of adaptation (black line) to a critical level (horizontal lines), a given change in the critical adaptation level primarily affects the duration of long perceptual epochs since those are associated a shallower part of the adaptation curve. See the main text for a more detailed explanation. (B) The fact that the predicted reversal of Proposition IV at very low stimulus strengths has been proven difficult to measure using luminance contrast as the independent variable, is consistent with the notion of a sharply saturating contrast transfer function of the early visual system. With such a transfer function the critical range of effective stimulus strengths is associated with a very narrow range of physical contrast levels. (C) The literature has shown the degree of symmetry of alternation rate around equidominance to be variable. The inset illustrates a manipulation that increases stimulus strength X from low to high levels while fixing stimulus strength Y either at a low level (black arrow) or at a high level (gray arrow). The open circles depict mirror situations where either stimulus X is weak and stimulus Y is strong (gray) or the other way around (black). The middle panel shows the most common result of such a stimulus strength manipulation. The offset between curves at equidominance (dashed line) corresponds to Proposition IV. The top panel depicts a situation where the effect of Proposition IV is minimal or absent, resulting in symmetry around equidominance. When the effect described in Proposition IV is exceptionally strong, the pattern in the bottom panel arises. Here, there is an extreme offset between the two curves at equidominance and the alternation rate no longer peaks at equidominance either. See main text for additional details.

analyses of the model conditions that need to be met for the proposition to hold (Curtu et al., 2008; Seely & Chow, 2011; Shpiro et al., 2007). Given that binocular rivalry does comply with the original proposition in the vast majority of experimental situations that have been tested, these analyses allow us to formulate an inference regarding the neural system responsible for binocular rivalry.

In the context of conceptualizations involving adaptation and mutual inhibition, one can in principle conceive of two types of perceptual alternations (Curtu et al., 2008; Seely & Chow, 2011; Shpiro et al., 2007; Wang & Rinzel, 1992). In one scenario, termed *escape*, a perceptual alternation ensues when adaptation of the suppressed population recovers to a critical point where the population overcomes the inhibition from the other population (as in the example above from Wilson, 2007). In the other scenario, termed *release*, an alternation is triggered when accumulating adaptation of the dominant population reaches a critical level, causing a quick drop in the dominant population's activity, thereby releasing the suppressed population from inhibition. It has been demonstrated that an increase in stimulus strength facilitates *escape* alternations, but prevents *release* alternations (Curtu et al., 2008; Seely & Chow, 2011; Shpiro et al., 2007). This is consistent with intuition: an increase in stimulus strength would move the suppressed population closer to the critical point where it can escape inhibition, but it would move the dominant population farther from the critical point where it releases inhibition. In other words, Proposition IV, by stating that an increase in stimulus strength promotes the occurrence of perceptual alternations, suggests that the immediate cause of a perceptual switch is a critical rise in the efficacy of the neural entity that corresponds to the suppressed percept (i.e. *escape*), rather than a drop in the efficacy of the other entity (indeed, the model used as an example above, which relies

on escape transitions, reproduces Proposition IV; Wilson, 2007). This would also seem consistent with the experimental finding that monocular contrast changes affect the timing of perceptual switches more strongly when applied to the suppressed stimulus than when applied to the dominant stimulus (Mueller & Blake, 1989).

We have already mentioned that the relation between stimulus strength and alternation rate that is described by Proposition IV might reverse at very low stimulus strengths (dashed curve in Fig. 3D). Following the above reasoning this would mean that, at those stimulus strengths, the immediate cause of a perceptual switch is a critical reduction in the efficacy of the neural representation of the dominant percept. Experimentally, evidence for such a reversal has been obtained in a situation involving rivalry between two monocular patterns of moving dots, but only when the experimental handle on stimulus strength was the patterns' motion content (Platonov & Goossens, 2013). Varying dot luminance contrast, on the other hand, did not reveal a reversal. The putative inference that can be drawn from this pertains to the contrast transfer function of the early visual system (Platonov & Goossens, 2013; see also Seely & Chow, 2011). In particular, the finding that the original Proposition IV applies to all measurable contrast values even though the data on motion content point to a limit to the proposition's validity, suggests that the function that maps contrast onto effective stimulus strength is strongly saturating (Fig. 6B). Consequently, the low range of stimulus strengths at which a reversal of Proposition IV would occur, corresponds to a very narrow range of physical contrasts that might be difficult to sample experimentally (or even impossible, in the case of random fluctuations in the effective stimulus strength and/or a non-zero level of its baseline).

7.3. Symmetry and normalization

Moreno-Bote et al. (2010) proposed that alternation rate not only peaks at equidominance, but is also symmetrical around that point when plotted as a function of predominance, as is approximately true in Fig. 4A and B. We opted not to include such symmetry as a general rule in the Modified propositions, because there are several counterexamples (e.g. Fig. 5). The notion of symmetry and Moreno-Bote and colleagues' associated discussion are nevertheless relevant. In fact, they lead to a tentative framework that might unify the various data patterns that have been discussed above.

Fig. 6C illustrates this framework, using the plotting format introduced in Fig. 5. We return to this plotting format here, because it will facilitate a comparison with the empirical data of Fig. 5. As illustrated by the top-right inset of Fig. 6C, each curve in Fig. 6C is associated with a change in the strength of a stimulus X, and the two shades indicate whether the strength of the other stimulus, Y, is low (black) or high (gray). We now also include an open dot at one end of each curve, as a reminder that those ends involve the same pair of stimulus strengths (but with labels X and Y flipped), which means that alternation rate should be identical at both those ends, and that both ends must also be located at an equal distance from the equidominance line (dashed). These constraints are then used to anchor the curves in the three plots of Fig. 6C. The middle panel of Fig. 6C essentially repeats Fig. 5A and illustrates the situation where Modified Propositions I–IV all hold. Although this is the most commonly observed situation for binocular rivalry, other data patterns have also been observed. In the experiments by Moreno-Bote et al. (2010) the relation between alternation rate and predominance was close to symmetrical around the point of equidominance. The top panel of Fig. 6C shows such a situation. As is clear from the panel, and as discussed by Moreno-Bote et al. (2010), such a large degree of symmetry requires the effect described by Proposition IV to be minimal (i.e., the distance between the black and gray curves at equidominance must be small). Perfect symmetry, in other words, is not consistent with the Modified Propositions (nor with the original ones). Other stimuli, notably large binocular rivalry stimuli (Kang, 2009) and the MIB/Troxler's fading stimuli of Bonneh et al. (2014, Fig. 5D), have produced a data pattern that deviates from that of the most common middle panel in a different way, which is illustrated in the bottom panel. For these stimuli, the alternation rates tend to increase monotonically with predominance rather than to peak at equidominance, which means the data complied with the original, rather than the modified, Proposition III (and II) in a relatively large part of the stimulus domain. As the bottom panel shows, this can be interpreted as a situation that is opposite to the fully symmetrical situation of the top panel in the sense that the effect described by Proposition IV is exceptionally large here.

To summarize, one could think of the patterns of behavior observed across ambiguous stimuli as ranging from cases where the effect described by Proposition IV is weak and alternation rate is near-symmetrical around equidominance (Fig. 6C, top), via the most common, intermediate, case where the Modified propositions apply (Fig. 6C, middle), to a case where the effect described by Proposition IV is strong and behavior comes closer to the original Propositions II/III (Fig. 6C, bottom). One benefit of this conceptualization is that the work of Moreno-Bote et al. (2010) suggests a straightforward way to traverse the continuum that connects the three patterns of behavior. Those authors point out that the symmetrical case naturally arises in a system where both stimuli that are involved in a competitive process, for instance the two monocular images in the case of binocular rivalry, feed into a common normalization pool that controls the effective strength of a stimulus (Carandini & Heeger, 2011). Take, for instance, the extreme scenario where the effective strength of X is obtained by

dividing the input strength of X by the sum of the input strengths of X and Y combined. One way of understanding why this leads to the data pattern in the top panel of Fig. 6C, is to realize that the manipulation underlying Proposition IV, a simultaneous and equivalent change in both stimulus strengths, will have no effect on effective strength in this scenario (its value will remain 0.5). More generally, if it is only relative, rather than absolute, strength that matters then plots like the ones in Fig. 6C must always be symmetrical because relative strength, as indexed by relative predominance, is symmetrical around equidominance in plots like these.

It is interesting to note that in MIB/Troxler's fading, which is perhaps the paradigm that produces the most strongly asymmetrical data pattern (Fig. 5D), the two competing stimuli (target and mask) occupy different regions of space. This is a fairly unusual situation among perceptual bistability paradigms. Since the normalization pool of a neuron is thought to primarily receive input from neurons that are responsive to stimulation within nearby regions of visual space (Carandini & Heeger, 2011), it is not unreasonable to expect a weaker normalization between the competing stimuli in MIB compared to other bistability phenomena. Moreover, for binocular rivalry the most symmetrical (Moreno-Bote et al., 2010) and the most asymmetrical (Kang, 2009) data patterns have been obtained using very small and very large stimuli, respectively, and one wonders whether this is related to the notion that normalization during binocular rivalry depends on stimulus size (Ling & Blake, 2012; see also Reynolds & Heeger, 2009).

Considering all the above, we will close this section with the following conjecture. In the absence of input normalization the neural interactions that underlie binocular rivalry and other bistable perceptual phenomena have a tendency toward the asymmetrical behavior illustrated in the bottom panel of Fig. 6C. The presence of input normalization in most cases causes behavior similar to that in the Fig. 6C's middle panel to arise as the most common result, and in more extreme cases it causes behavior like that in Fig. 6C's top panel. This idea, although speculative, is worth considering because it suggests a plausible single explanation for the range of distinct data patterns observed in various experiments.

8. General applicability

Levelt formulated his propositions specifically with binocular rivalry in mind. The Modified propositions that we presented here are also tailored to that particular paradigm, because capturing the variety of findings from other paradigms would require too many qualifying clauses. Nevertheless, the overwhelming sense from the literature, summarized in Figs. 4 and 5, is of a fundamental similarity across paradigms, sometimes obscured by differences in detail. The suggestions in our previous section may go some way toward explaining those differences, but the fundamental similarity exists regardless. The exciting implication is that the neural network engaged during binocular rivalry, while plausibly involved in the processes of binocular combination and fusion that were the focus of Levelt's original work, also shares key features with the networks involved in other forms of bistable perception (see also Andrews & Purves, 1997; Klink, Van Ee, & Van Wezel, 2008; Leopold & Logothetis, 1999; Schwartz et al., 2012).

The data we discussed add to a plethora of known similarities between binocular rivalry and other forms of perceptual bistability. One striking example that is reviewed elsewhere (Pearson & Brascamp, 2008), is the characteristic way, similar across many bistable perception paradigms, in which prior encounters with a given stimulus influence its perception upon reappearance (Klink, Van Ee, Nijs, et al., 2008; Leopold et al., 2002). Another example is

the way in which spatial context affects the perceptual dynamics associated with these stimuli (Klink et al., 2012). A more in-depth review and discussion of similarities between different forms of bistability can be found in Schwartz et al. (2012).

A considerable number of recent studies have focused on perceptual bistability outside of vision, namely in the domains of audition (Davidson & Pitts, 2014; Denham & Winkler, 2006; Hupé, Joffo, & Pressnitzer, 2008; Moore & Gockel, 2012; Pressnitzer & Hupé, 2006; Snyder, Carter, et al., 2009), haptics (Carter et al., 2008; Holcombe & Seizova-Cajic, 2008), proprioception (Holcombe & Seizova-Cajic, 2008) and olfaction (Zhou & Chen, 2009). This work has again underscored the generality of some of the findings we discussed, by revealing striking parallels with visual bistability (Carter et al., 2008; Davidson & Pitts, 2014; Holcombe & Seizova-Cajic, 2008; Hupé et al., 2008; McKendrick et al., 2011; Pressnitzer & Hupé, 2006; Snyder, Holder, et al., 2009; Snyder, Carter, et al., 2009). The work has also suggested experimental handles that might be used to control stimulus strength in non-vision paradigms, inviting a systematic evaluation of Levelt's propositions outside of the visual domain. However, such an evaluation has, to our knowledge, not yet been performed.

While all these similarities between different forms of perceptual bistability do not necessarily imply that a single neural structure is responsible for the perceptual alternations in each of these phenomena, they do suggest that the neural system exposed so vividly by binocular rivalry has canonical characteristics that are widespread throughout the sensory brain, and that come to light whenever sensory input is ambiguous.

9. Future directions

In this review we have discussed existing knowledge on the relation between stimulus strength and percept dynamics during bistable perception, originally embodied in Levelt's propositions and refined in more recent years. This discussion revealed many aspects in need of further investigation. For instance, the theoretically important possibility that Proposition IV may break down at low stimulus strengths has hitherto received only limited empirical verification (Platonov & Goossens, 2013). Also, it remains to be seen what underlying mechanisms cause data from various bistability paradigms to differ in their degree of symmetry (Fig. 6C), and whether this is indeed related to differences in input normalization. Another important question is whether the characteristics reviewed above apply to forms of perceptual bistability outside of vision. This question seems addressable using existing experimental methods, and an affirmative answer would demonstrate even greater generality of the neural properties that are uncovered by bistable perception paradigms.

Beyond such investigations, which are similar in spirit to the work discussed in this review, a major challenge for future research is to integrate this type of work with results from other subfields. The evidence reviewed above, by demonstrating the ubiquitous appearance of the same computational principles across stimuli that engage different parts of the visual brain and different aspects of perceptual organization, highlights the value of such integration for understanding brain function. It is often unclear, however, how to translate findings from the present subfield to domains that do not involve bistability or, indeed, how to interpret such findings in neural terms. For instance, computational models of the kind discussed in Section 7 are unparalleled in their ability to concisely capture psychophysical findings on perceptual bistability, and they provide a powerful tool for interpretation that we gratefully employed above. At the same time, current models of this kind are quite limited in their ability to explain findings outside of bistable perception, a type of generalization that would

be very helpful in situating the system probed by bistable perception paradigms within the neuroscience of perception more generally (e.g. Said & Heeger, 2013). Similarly, several studies have framed perceptual bistability in terms of general principles of perceptual inference (Hohwy et al., 2008; Kanai, Carmel, Bahrami, & Rees, 2011; Sundaeswara & Schrater, 2008), yet these conceptualizations do not have the same degree of predictive power as the existing computational models discussed above. This raises the question whether the structure of computational models of the kind discussed in Section 7 can be recast in terms of such a more general conceptual framework, thereby combining predictive power with broad applicability. On a final related note, some existing work has started to link the components that make up models of bistable perception, such as 'adaptation' and 'inhibition', to empirical measures of neural function, and to combine the collection of such measures with the parametric approach characteristic of the psychophysical studies discussed above (e.g. Donner, Sagi, Bonnef, & Heeger, 2013; Moradi & Heeger, 2009; van Loon et al., 2013). This direction of research appears especially promising, because a more direct link with the neural substrate would bolster the power of psychophysical and computational work in Levelt's tradition, and further increase its value for the neuroscientific study of perception.

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