



Minireview

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

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ARTICLE INFO

Article history:

Received 3 January 2015

Received in revised form 13 February 2015

Available online 4 March 2015

Keywords:

Vision

Perception

Binocular rivalry

Bistable perception

Psychophysics

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

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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,

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