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Individual differences in sensory eye dominance reflected in the dynamics of binocular rivalry

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ABSTRACT

Normal binocular vision emerges from the combination of neural signals arising within separate monocular pathways. It is natural to wonder whether both eyes contribute equally to the unified cyclopean impression we ordinarily experience. Binocular rivalry, which occurs when the inputs to the two eyes are markedly different, affords a useful means for quantifying the balance of influence exerted by the eyes (called *sensory eye dominance*, SED) and for relating that degree of balance to other aspects of binocular visual function. However, the precise ways in which binocular rivalry dynamics change when the eyes are unbalanced remain uncharted. Relying on widespread individual variability in the relative predominance of the two eyes as demonstrated in previous studies, we found that an observer's overall tendency to see one eye more than the other was driven *both* by differences in the relative duration and frequency of instances of that eye's perceptual dominance. Specifically, larger imbalances between the eyes were associated with longer and more frequent periods of exclusive dominance for the stronger eye. Increases in occurrences of dominant eye percepts were mediated in part by a tendency to experience "return transitions" to the predominant eye – that is, observers often experienced sequential exclusive percepts of the dominant eye's image with an intervening mixed percept. Together, these results indicate that the often-observed imbalances between the eyes during binocular rivalry reflect true differences in sensory processing, a finding that has implications for our understanding of the mechanisms underlying binocular vision in general.

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1. Introduction

Under ordinary viewing conditions, binocular visual perception belies little hint of its dual monocular origins – it feels as if we're seeing the world through a single, cyclopean eye. Yet because the earliest stages of visual processing are patently monocular, it is feasible that the two eyes might contribute differentially to the perceptual experience, culminating from the processes promoting binocular combination. It is known, for example, that optical aberrations can differ between the two eyes of some individuals (Porter, Guirao, Cox, & Williams, 2001). Moreover, neural processing in the retina, in the thalamus, and in layer 4 of the primary visual cortex is accomplished largely by neurons that respond to inputs originating in one eye or the other but not both (Squire et al., 2003). Differential contributions from the two eyes might also arise within cortical neural mechanisms directly involved in binocular combination (Cumming & DeAngelis, 2001). It is under-

standable, therefore, that some vision scientists are interested in establishing methods for determining the extent to which binocular vision is impacted by the level of balance between the contributions from the left eye (LE) and the right eye (RE).

One broad category of methods used to assess the relative impact of the two eyes on binocular vision measures an observer's reliance on one eye over the other for aligning targets in the environment, i.e., sighting dominance (e.g. Fink, 1938). Other measures focus on differences between the eyes in monocular acuity and contrast sensitivity (e.g. Suttle et al., 2009). By and large these methods have proven rather unreliable (e.g. Banks, Ghose, & Hillis, 2004; Khan & Crawford, 2001), and they tend to be unrelated to one another and/or to other binocular visual functions (Ehrenstein, Arnold-Schulz-Gahmen, & Jaschinski, 2005; Mapp, Ono, & Barbeito, 2003; Pointer, 2007; Rice, Leske, Smestad, & Holmes, 2008).

A technique that has proven successful at both measuring differences between the eyes and relating these to the quality of binocular vision is binocular rivalry. The conditions instigating binocular rivalry are created by dichoptic presentation of conflicting visual stimuli to the two eyes, thereby provoking reciprocal,

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alternating periods of perceptual dominance and suppression between the two stimuli when they are viewed for an extended period of time (Alais, 2012; Blake & O'Shea, 2009). Importantly, the amount of time that one or the other monocular stimulus is seen depends on the relative salience of the two stimuli. Thus, for example, a high contrast stimulus will predominate over a lower contrast stimulus (Brascamp, van Ee, Noest, Jacobs, & van den Berg, 2006; Levelt, 1968) and a well-focused stimulus will predominate over a blurred one (Arnold, Grove, & Wallis, 2007). Similar biases in dominance are observed when disparities in monocular salience arise from intrinsic differences between the eyes, even when the stimuli being viewed by the LE and RE are equal in physical strength (Handa et al., 2004; Porac & Coren, 1978). One can systematically manipulate the contrast or the luminance of the stimulus viewed by the disadvantaged eye to achieve equal predominance during rivalry, thus acquiring a quantitative metric of *sensory eye dominance* (SED; Ooi & He, 2001). This metric is predictive of binocular visual performance in a stereoacuity task (Xu, He, & Ooi, 2011), and, when used to determine eye assignment for monovision correction (i.e., purposefully imbalanced refractive correction of the two eyes allowing distance vision by one eye and near vision for the other, sometimes favored by presbyopes or by patients following cataract surgery), this information can help improve binocular contrast sensitivity (Zheleznyak, Alarcon, Dieter, Tadin, & Yoon, 2015).

These promising links between SED and measures of binocular visual function point to the potential utility of binocular rivalry for assessing individual differences in binocular function. However, it remains unknown exactly how imbalances in eye dominance affect the dynamics of ongoing binocular rivalry in order to promote increased predominance of the dominant eye. Specifically, some previous methods have relied primarily on brief presentations of dichoptic stimulation (Ooi & He, 2001; Xu, He, & Ooi, 2012; Xu et al., 2011). Such methods target onset rivalry, a brief period of time (~1 s) following the initial presentation of dichoptic stimuli that is characterized by an increased influence of factors such as attention and color on rivalry predominance (Carter & Cavanagh, 2007; Mitchell, Stoner, & Reynolds, 2004; Stanley, Forte, Cavanagh, & Carter, 2011). Others have focused on the overall predominance of one eye across an extended binocular rivalry-tracking period (Handa et al., 2004; Porac & Coren, 1978; Zheleznyak et al., 2015). Importantly, there are a variety of ways that binocular rivalry dynamics could be altered that would yield a larger proportion of viewing time for one eye during an extended tracking block. These include changes in the relative frequency and/or duration of LE versus RE percepts (and relatedly, changes in alternation rate), and/or a reduction in the frequency or duration of periods of mixed perception.

As such, while these methods manifestly provide a useful measure of the differences between the eyes, we sought to identify precisely *how* eye dominance alters binocular rivalry dynamics in order to give rise to the sometimes profound predominance of one or the other eye. Given the wide degree of individual variability in SED observed in previous studies (Al-Dossari, Blake, Brascamp, & Freeman, 2015; Ooi & He, 2001; Xu et al., 2011; Yang, Blake, & McDonald, 2010), we tested a large sample of observers and utilized an individual differences approach to identify signatures of SED in the dynamics of ongoing binocular rivalry. This allowed us to investigate both the variability in SED extent across our sample, as well as to relate each observer's SED to particular characteristics of binocular rivalry dynamics. By focusing on signature changes in rivalry dynamics that are associated with SED, we hoped to gain insights into the nature of eye dominance's impact on visual perception. For example, Levelt's early work carefully described expected changes in dynamics when one of the rival images is raised or lowered in contrast (Levelt, 1968), and our

study offers the possibility of revealing important correlates of these patterns (also see Brascamp et al., 2006). In addition, quantifying the prevalence and extent of imbalances between the eyes during binocular rivalry across our sample of observers will be an important finding for those using binocular rivalry (and related methods involving interocular suppression, such as continuous flash suppression, Tsuchiya & Koch, 2005) to compare the visual properties of different classes of images. Researchers seek to attribute measured differences to the images themselves rather than to intrinsic differences between the eyes; yet, it is possible that SED could impact these results.

2. Method

2.1. Observers

89 observers (56 females, 33 males; median age 24 ± 11.4 yrs; range 18–68 yrs) participated in the study. These volunteers were recruited through advertisements posted in the Vanderbilt University Psychology Sign-Up System and the Vanderbilt Kennedy Center "Study Finder." Two observers (KD & JS) are also authors. Based on prescreening conversations, all other observers had little or no prior experience viewing binocular rivalry, and they remained naïve as to the purpose of this study until after they completed it. Each observer reported normal or corrected to normal vision; however, three observers were excluded from analysis because laboratory measurements revealed monocular acuity in one eye that was worse than 40/20. One additional observer was excluded because he revealed after testing that he had monovision correction. All procedures were approved by the Vanderbilt University Human Research Protection Program, and each observer provided written informed consent prior to participation. This work was carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

2.2. Apparatus

Stimuli were generated using the MATLAB Psychophysics Toolbox (Brainard, 1997). They were presented on a linearized Sony CPD-E540 monitor (1024×768 resolution) running at 100 Hz. Observers viewed stimuli through a mirror stereoscope that was mounted on a chin rest, fixed 80.5 cm from the display (viewing distance through the mirrors).

2.3. Stimuli

To induce binocular rivalry, observers foveally viewed orthogonal sine wave gratings (± 45 degrees; 1.5 dva circular diameter; 30% contrast; 3 cyc/deg). The eye-to-stimulus pairing was alternated across ten 60-s tracking blocks. Rival targets were surrounded by identical fusion stimuli consisting of a clutter of overlapping circles presented in the background viewed by each eye, the presence of which promoted stable binocular eye alignment throughout the experiment.

2.4. Procedure

Before beginning the binocular rivalry tracking experiment, observers completed a custom alignment procedure in which they used key presses to move LE and RE fusion stimuli on the screen (identical to those used in the tracking experiment, except without rival gratings) to positions where they remained aligned when using a version of the cover/uncover test. This process was completed three times, with the average LE and RE image coordinates then used to position the rival images on the screen during the

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