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Infants' responsiveness to rivalrous gratings

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ABSTRACT

The study investigated the early development of responsiveness to rivalrous gratings. Infants were tested weekly between 6 and 16 weeks of age for their ability to discriminate between interocularly identical (fusible) lines and interocularly orthogonal (unfusible, rivalrous) lines. The stimuli were presented on an autostereoscopic monitor equipped with a face-tracking device. Two psychophysical techniques, the forced-choice preferential looking (FPL) method and measurement of looking times, were employed. Contrary to earlier findings, infants at all ages avoided looking at the rivalrous gratings instead of showing a developmental shift from a relative preference for unfusible, rivalrous gratings to a relative preference for fusible gratings. Avoidance of the rivalrous gratings became significant at 8–9 weeks of age, suggesting that infants clearly exhibit binocular rivalry from that age onwards. Control experiments secured that the infants' preference for the fusible gratings was not governed by a natural preference for less over more complex line patterns.

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1. Introduction

Binocular rivalry occurs when the eyes receive a pair of images that cannot be fused into a coherent perception. The neurocognitive mechanisms of binocular rivalry are under debate (for reviews, see Blake & Logothetis, 2002; Tong, Meng, & Blake, 2006). One opinion is that binocular rivalry is a low-level process, arising from interocular competition between monocular neurons in V1 or in the lateral geniculate nucleus. Research on adult humans and on non-humans suggests that these areas play a crucial part in binocular rivalry (e.g., Leopold & Maier, 2006; Maier et al., 2008; Pitts, Martínez, & Hillyard, 2010). Alternatively, binocular rivalry is assumed to be a high-level process, occurring in higher sites of the visual pathway and arising from competition between incompatible stimulus patterns. Neurophysiological evidence indicates that multiple cortical areas are activated in the human brain during binocular rivalry, including parietal (e.g., Britz, Pitts, & Michel, 2011), temporal (e.g., Cosmelli et al., 2004), and frontal areas (e.g., Wilcke, O'Shea, & Watts, 2009).

Simple patterns like gratings generate shallow, incomplete suppression and piecemeal rivalry. Piecemeal rivalry can be evoked, for example, by sending gratings with differential orientations to the two eyes. Typically, interocularly orthogonal gratings are used in which horizontal lines are sent to one eye and vertical lines are sent to the other. Interocular orthogonal gratings elicit the perception of a fluctuating patchwork of lines, fragmented alternations, in which one half-image dominates some parts of the image while the other half-image dominates other parts (e.g., Alais, 2012).

Physiological and behavioral indicators have been applied in research on infant sensitivity to binocular rivalry. This research indicates responsiveness to binocular rivalry as early as 3 months of age. In physiological studies, binocular functioning has been assessed by measuring visual evoked potentials (VEPs) in response to different kind of stimuli. Braddick et al. (1980) found evidence for cortical binocularity in infants tested with a dynamic random dot correlogram (RDC). In the dynamic RDC, the dot pattern alternated rapidly between a correlated and an anticorrelated phase. In the correlated phase, the images presented to the eyes were identical. In the anticorrelated phase, the image presented to one eye was the negative of that presented to the other eye. Differential VEPs to the two phases indicate that the visual system detects whether (correlated pattern) or not (anticorrelated pattern) the images sent to each eye can be fused. Braddick et al. (1980) established that, in general, by the age of 3 months infants respond sensitively to the dynamic RDC. Several studies have confirmed this finding (e.g., Braddick et al., 1983; Petrig et al., 1981; Skarf et al., 1993). Birch and Petrig (1996) demonstrated that responsiveness to correlated versus anticorrelated patterns increased from 2 to 8 months of age as indicated by both VEP and preferential looking.

VEPs to dichoptic, interocularly orthogonal striped patterns have been measured by Brown, Candy, and Norcia (1999). Inconsistent with the results from RDC studies, infants 5–15 months of age failed to demonstrate physiological rivalry.

Higher level of VEPs to phase-alternating patterns under binocular viewing in contrast to monocular viewing is an index of binocular summation, the integration of binocular inputs. Binocular



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summation has been observed in infants from approximately 2 months of age onwards (e.g., Amigo et al., 1978; Leguire, Rogers, & Bremer, 1991; Penne et al., 1987; Shea, Aslin, & McCulloch, 1987).

Odom and Harter (1983) have investigated interocular suppression, the reduced visibility of a stimulus presented to one eye by a stimulus presented to the other eye. Interocular suppression in infants 3 months of age and in adults was assessed by VEP signals. The magnitude of interocular pattern suppression in infant participants was comparable to that in adult participants.

Consistent with the studies using electrophysiological techniques, behavioral studies have shown that from approximately 3 months onwards infants prefer fusible over rivalrous gratings (Birch, Shimojo, & Held, 1985; Gwiazda, Bauer, & Held, 1989; Shimojo, 1993; Shimojo et al., 1986; Thorn et al., 1994). Gwiazda, Bauer, and Held (1989) presented two stimuli to infants, one of which consisted of interocularly identical vertical gratings (fusible stimulus) and the other of interocularly orthogonal gratings (unfusible stimulus). Only the unfusible stimulus generates piecemeal binocular rivalry in adults. The infants were tested repeatedly between approximately 3-20 weeks age. Gwiazda, Bauer, and Held (1989) examined visual preference toward the stimuli with the forced-choice preferential looking (FPL) method (e.g., Teller, 1997). In a test session, the fusible and the unfusible stimuli were repeatedly shown. At each stimulus presentation trial, an observer judged which stimulus the infant had attended to. Gwiazda, Bauer, and Held (1989) found an age-related shift from a relative visual preference for the interocularly orthogonal gratings to a relative preference for the interocularly identical gratings. Mean age of onset of relative preference for the fusible stimulus was 12.4 weeks of age. Moreover, a sex difference occurred. Females exhibited a mean onset of relative preference for the fusible gratings at 9.9 weeks, males at 13.8 weeks. Similar findings have been obtained by Shimojo et al. (1986; see also Shimojo, 1993).

According to a common explanation, the preference for a fusible over a rivalrous target displayed from 3 months of age onwards indicates maturation of the neurophysiological mechanisms of binocularity: The visual system becomes adult-like and extracts rivalry. Rivalrous stimuli are assumed to be aversive for infants. As a consequence, with the onset of binocularity, infants avoid looking at the interocularly orthogonal gratings and direct their attention to the interocularly identical gratings.

Younger infants' preference for the rivalrous over the fusible stimulus is explained by the "superposition hypothesis" (e.g., Held, 1991, 1993). According to this hypothesis, the signals from the two eyes are nonselectively combined into a single, uniform representation in the younger infants' immature visual system. More specifically, interocularly orthogonal gratings are summed up and the stimulus is perceived as a lattice. Since infants tend to prefer looking at complex patterns, they look longer at the lattice than at an interocularly identical (vertical or horizontal) gratings stimulus. Held (e.g., 1993) delineates that the axons from both eyes are connected with the same cells in layer IV of young infants' primary visual cortex (V1). As a result, the signals from the two eyes are blended. Rivalry emerges when the afferent nerves from both eyes are segregated in layer IV.

Several studies have criticized the hypothesis of superposition of inputs from the two eyes in young infants. In macaque monkeys, disparity sensitive anatomical structures in V1 and V2 are present from an early age onwards (e.g., Endo et al., 2000; Horton & Hocking, 1996; Maruko et al., 2008). Endo et al. (2000) found that V1 neurons in young infant monkeys are capable of initiating interocular suppressive interactions which are a prerequisite for binocular rivalry. These interactions were stronger than those in adult monkeys before 8 weeks of age. In sum, by indicating the early presence of rivalry-related binocular mechanisms, neurophysiological findings do not support the superposition hypothesis.

Braddick (1996) points out that the superposition hypothesis is not consistent with infant responsiveness to dynamic random dot correlograms. Under dichoptic presentation RDC are perceived to alternate between fusible and non-fusible patterns in adults. If the random dot patterns are not separated between the eyes (non-dichoptic presentation), the rapid transitions between correlation and anticorrelation are perceived as transitions between low- and high-contrast dots. Accordingly, if the young infants' visual system sums the signals from the two eyes, as proposed by the superposition hypothesis, dynamic RDC would elicit similar VEPs under dichoptic and non-dichoptic presentation. Binocular VEP responses to dichoptically presented RDC would appear later. Contrary to this prediction, Braddick et al. (1983) observed strong VEPs under non-dichoptic but not under dichoptic viewing in infants younger than approximately 3 months.

Finally, in human infants 5–16 weeks of age, Brown and Miracle (2003) did not find evidence for a preference of interocularly orthogonal gratings over interocularly identical horizontal gratings. With age, the infants increasingly preferred the interocularly identical gratings over the rivalrous gratings. Again, this behavioral finding disconfirms the superposition hypothesis.

The primary goal of the study was to examine whether a developmental shift from a relative preference for rivalrous to a relative preference for fusible gratings occurs at approximately 12– 14 weeks, as suggested by earlier studies. The study extends the investigation conducted by Brown and Miracle (2003) by applying two experimental methods, the FPL method (Experiment 1) and the classical natural preference (CNP) method (Experiment 2). In the CNP method, the distribution of looking times across two stimuli is measured. Moreover, the stimuli were displayed on an autostereoscopic monitor equipped with a face-tracking device. Glasses to separate the views of the eyes were not needed.

The superposition hypothesis assumes that young infants prefer dichoptic gratings over fusible gratings because the dichoptic pattern is blended into a complete lattice, which is more complex than the fusible gratings. However, research on preferential looking at complex patterns provides evidence that infant looking is modulated by an interaction between complexity and age (e.g., Brennan, Ames, & Moore, 1966; Horowitz, Tims, & McCluskey, 1974). In additional samples, it was therefore examined whether infants prefer a (complex) lattice over horizontal lines. Again, two samples were followed longitudinally, one using the FPL (Experiment 3) and one using the CNP technique (Experiment 4).

2. Experiment 1: Rivalrous gratings versus fusible gratings. Forced-choice preferential looking

2.1. Methods

2.1.1. Participants

Twenty-four full-term, healthy infants (12 girls and 12 boys) comprised the sample. The infants were recruited by letter and follow-up telephone calls. The infants also participated in a CNP experiment on sensitivity to horizontal disparity (Kavšek, submitted for publication). The names of the infants were obtained from birth records provided by the municipal authorities of the City of Bonn (Bonn, Germany). Data protection was guaranteed. The parents were paid 5 Euros at each visit. Additionally, after the last test session, they were given a compact disk containing all recordings showing their infant. Parents were informed about the study and gave informed consent before onset of the first testing. The study was approved by the ethics committee of the Institute of Psychology at the University of Bonn.

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