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A theory of the visual system biology underlying development of spatial frequency lateralization

Mary F. Howard [a,*], James A. Reggia [b]

[a] Department of Biology, University of Maryland, Biology & Psychology Building, Room # 3205, College Park, MD 20742, USA
[b] Departments of Computer Science and Neurology, Institute for Advanced Computer Studies, University of Maryland, College Park, MD, USA

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Abstract

The spatial frequency hypothesis contends that performance differences between the hemispheres on various visuospatial tasks are attributable to lateralized processing of the spatial frequency content of visual stimuli. Hellige has proposed that such lateralization could arise during infant development from the earlier maturation of the right hemisphere combined with the increasing sensitivity of the visual system to high spatial frequencies. This proposal is intuitively appealing but lacks an explicit theory with respect to the underlying visual system biology. In this paper, we develop such a theory based on knowledge of visual system processing and development. We then translate our theory into a computational model that serves as the basis for a series of development simulations. We find that the simulations produce spatial frequency lateralization effects consistent with those observed empirically. We relate the nature of the neural asymmetry implied by our theory to empirical findings on visual pathway bias and the relative spatial frequency lateralization effect.

Keywords: Spatial frequency; Hemispheric asymmetry; Lateralization; Visual development; Computational model

1. Introduction

Numerous lesion studies and psychophysical experiments offer convincing evidence that the right and left hemispheres differ in their performance on various visuospatial tasks (for reviews see Hellige, 1993; Ivry & Robertson, 1998). The spatial frequency hypothesis (Sergent, 1982, 1987) contends that many of the performance differences found on seemingly unrelated tasks are attributable to a common underlying cause: the lateralized processing of the spatial frequency content of visual stimuli. It further contends that the initial "sensory" processing of a visual stimulus is symmetric and that the lateralization, characterized as the more efficient processing of the low spatial frequency content of a stimulus by the right hemisphere and the high spatial frequency content by the left hemisphere, arises in the processing that takes place beyond that point. The existence of this hypothesized processing asymmetry is supported by the findings of extensive observational research (for reviews see Christman, 1997; Grabowska & Nowicka, 1996; see also Peyrin, Chauvin, Chokron, & Marendez, 2003). In particular, psychophysical experiments that measured reaction time on identification tasks involving peripheral presentation of gratings of known spatial frequency to right-handed subjects produced the expected lateralization effects (Christman, Kitterle, & Hellige, 1991; Kitterle, Christman, & Hellige, 1990; Kitterle, Hellige, & Christman, 1992; Kitterle, Christman, & Conesa, 1993; Kitterle & Selig, 1991; Proverbio, Zani, & Avella, 1997). In these experiments, processing involving low frequencies (<2 cycles per visual degree) produced faster reaction times for right hemisphere/left visual field (RH/LVF) presentation, while processing involving high frequencies (>3 cycles per visual degree) produced faster reaction times for left hemisphere/right visual field (LH/RVF) presentation. The magnitude of lateralization observed

* Corresponding author. Fax: +1 301 314 5052.
E-mail address: mfhoward@umd.edu (M.F. Howard).

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was typically small—less than ±0.05 when quantified using the asymmetry coefficient $\sigma = (t_R - t_L)/(t_R + t_L)$ where t_R and t_L are the reaction times for RH/LVF and LH/RVF presentation, respectively (Lezak, 1995)—but generally statistically significant.

An explanation of how such asymmetry in the processing of spatial frequencies could arise has been proposed by Hellige (1993, 1995, 1996, 2006). He hypothesized that the co-occurrence of two conditions in the neonate leads to the development of spatial frequency lateralization: the earlier maturation of the right hemisphere and the increasing sensitivity of the visual system to high spatial frequencies. Earlier maturation of the right hemisphere is supported by both anatomical and imaging evidence (Bracco, Tiezzi, Ginanneschi, Campanella, & Amaducci, 1984; Chi, Dooling, & Gilles, 1977; Chiron et al., 1997; Dooling, Chi, & Gilles, 1983; Scheibel, 1984; Gupta et al., 2005). Increasing sensitivity of the visual system to high spatial frequencies is supported by evidence from psychophysical and electrophysiological studies on infants (Banks & Dannemiller, 1987; Dobson & Teller, 1978; Gwiazda, Bauer, Thorn, & Held, 1997; Kelly, Borchert, & Teller, 1997; Norcia, Tyler, & Hamer, 1990) and is thought to be mainly attributable to retinal maturation (Youdelis & Hendrickson, 1986). Hellige argued that because the sensitivity of the neonatal visual system is limited to the low end of the spatial frequency range, the earlier developing right hemisphere acquires a specialization for processing low frequency input. Furthermore, because of improving visual system sensitivity to high spatial frequencies, the later developing left hemisphere acquires a specialization for the processing of high spatial frequency input. Hellige suggested that the developmental scenario may involve an interaction between the time course of visual development and the timing of "critical periods" of intense synaptic modification in the two hemispheres.

This proposal has intuitive appeal but lacks an explicit theory with respect to the underlying visual system biology. The goal of the work presented here is to develop such a theory based on current findings on visual system processing and development. In particular, we identify a set of visual system components and processes that could hypothetically work in combination with asynchronous hemispheric development to bring about the development of spatial frequency lateralization. We then provide a more definitive interpretation of our theory by specifying it as a computational model. Finally, we show that development simulations based on the model produce spatial frequency lateralization effects consistent with those observed empirically.

The modeling simulations can be viewed as an extension of our earlier work that demonstrated the potential for asynchronous hemispheric development to produce functional lateralization (Howard & Reggia, 2004). In that modeling study, which examined the relationship between the timing of task learning and the state of hemispheric plasticity, we showed that differences in the timing of task learning periods, coupled with differences in the timing of plasticity for the two hemispheres, produced oppositely directed lateralization for two distinct tasks. The timing of the task learning periods was controlled by changing the stimuli presented to the network over time, thus changes external to the system played a critical role in eliciting the lateralized development. In this study, we show that change internal to the system that affects the input to asynchronously developing cortical areas can produce lateralized development in the absence of any change in the external stimuli. Conceivably, this set of circumstances could arise not only during early visual system development, but also throughout the course of cortical development, contributing significantly to the lateralization of cognitive functions.

2. Theory description and rationale

Our theory is built on the finding that each retinotopic location is represented in layer 2/3 of the primary visual cortex (V1) by a set of cells that respond as selective filters in the spatial frequency domain (for in-depth discussion see De Valois & De Valois, 1988). Because the peak frequencies of these filters cover an approximately six-octave range (0.5–16.0 cycles per degree) and the mean bandwidth is approximately 1.4 octaves (De Valois, Albrecht, & Thorell, 1982), filters that respond best to low spatial frequencies are distinct from those that respond best to high frequencies. V1 filters form feed-forward connections to V2 cells in the visual system's ventral pathway, which mediates pattern identification and discrimination tasks (Livingstone & Hubel, 1988). Clearly, these feed-forward connections could produce frequency lateralization effects under discussion if connections from low frequency filters were relatively stronger in the right hemisphere, while connections from high frequency filters were relatively stronger in the left hemisphere. Motivated by this prospect, we next consider whether the postnatal increase in sensitivity to high spatial frequencies, in conjunction with the later development of the left hemisphere, can drive the development of this sort of hard-wired asymmetry in connection strengths.

Asymmetry in filter connectivity could emerge from an initially symmetric state if two conditions apply. First, V1 filters compete for connectivity to V2 cells such that connections from filters that contribute most to V2 cell activation strengthen at the expense of connections from filters that contribute least (competitive Hebbian development). Second, high frequency filters compete more effectively for connections to V2 cells during the later left hemisphere development than during the earlier right hemisphere development. The first condition is consistent with findings that indicate activity-driven development of a Hebbian nature occurs in the visual cortex (Kirkwood & Bear, 1994). The second condition could arise if the activity of high frequency filters increases relative to that of low frequency filters as the visual system matures.

The postnatal increase in sensitivity to high frequencies is consistent with a change in relative filter activity, but