Vision Research 133 (2017) 12–20

Contents lists available at ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

Development of contrast normalization mechanisms during childhood and adolescence

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ARTICLE INFO

Article history:
Received 15 July 2015
Received in revised form 21 March 2016
Accepted 28 March 2016

Keywords:
Visual development
Contrast sensitivity
VEP
Gain control
Contrast normalization mechanisms

ABSTRACT

Contrast sensitivity is regulated by neural mechanisms that flexibly adjust responsiveness to optimize stimulus encoding across different environments. Here we studied the developmental status of gain control mechanisms in school-age children (5–17 years) and adults using a visual masking paradigm. A variable contrast, spatially random 2-D noise test pattern was masked by the presence of a superimposed independent noise pattern presented at 0, 12 and 40% contrast. Frequency-tagged steady state visual evoked potentials were used to separately record responses to the test (5.14 Hz) and the mask (7.2 Hz). By incrementally increasing the test contrast we measured contrast response functions for each mask contrast. The unmasked contrast response functions were largely similar in shape across age, but peak amplitude was higher in the children. Masking shifted the contrast response function rightward on the contrast axis in both the adults and older children, elevating contrast thresholds by a similar factor across age. However, in younger children, masking resulted in a change in the slope of the contrast response function. These findings suggest that immaturity in the contrast normalization process persists until approximately 11 years of age.

1. Introduction

Contrast sensitivity fundamentally limits downstream perceptual processes. Understanding contrast sensitivity in the normal environment with its wide range of input levels requires knowledge not only of the processes that fundamentally limit contrast thresholds such as photon efficiency and internal noise, but also the processes by which sensitivity is regulated over wide ranges of input intensity. Early in life, contrast sensitivity is poor and both photon inefficiency and high levels of internal noise have been implicated as playing important roles in limiting threshold sensitivity (Brown & Lindsey, 2009). Less is known about how threshold sensitivity is adjusted under different environmental conditions and how responsivity above threshold is regulated.

Beyond the initial transduction process, contrast sensitivity and supra-threshold responsivity are regulated through a variety of control mechanisms at different levels of the visual pathway. One computational goal is to adjust neural responses in way that maximizes the dynamic range of the response to varying input levels. These regulatory processes begin with light adaptation in the retina and extend into the LGN and cortex where sensitivity to environmental contrast is regulated (Brown, Lindsey, McSweeney, & Walters, 1995; Bonin, Mante, & Carandini, 2006; Scholl, Latimer, & Priebe, 2012; Shapley & Victor, 1978). In V1, responses to high contrast stimuli do not grow without bound, but saturate at high input levels, yielding a range over which responses increase monotonically with increasing contrast (Albrecht & Hamilton, 1982; Tolhurst, Movshon, & Thompson, 1981). Contrast gain control mechanisms shift the non-saturated portion of the neural response as a function of the prevailing image contrast. A particularly effective way of studying this regulatory process is by measuring the contrast response function of a neuron in the presence of a second "masking" stimulus of different contrasts (Bonds, 1989; Carandini, Heeger, & Movshon, 1997). Maskers are a form of environmental context and their use has provided many insights into contrast sensitivity starting with early psychophysical studies (Legge & Foley, 1980).

Most of what we know about the transfer of visual contrast information during development comes from measures of threshold sensitivity rather than of supra-threshold gain. Many measurements of contrast sensitivity in the developing human visual

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http://dx.doi.org/10.1016/j.visres.2016.03.010
0042-6989/

system have been made during infancy using psychophysical (Atkinson, Braddick, & Braddick, 1974; Banks & Salapatek, 1976; Banks & Stephens, 1982; Bonin et al., 2006; Dobkins & Teller, 1996), Visual Evoked Potential (Harris, Atkinson, & Braddick, 1976; Norcia, Tyler, & Hamer, 1990; Pirchio, Spinelli, Fiorentini, & Maffei, 1978) and eye movement measures (Brown et al., 1995; Hainline & Abramov, 1997; Meijer & van den Berg, 1982). These early contributions have shown that contrast sensitivity at low spatial frequencies develops quickly and is almost adult like at 6 months of age when measured using the VEP or eye-movements. Grating acuity, effectively a measure of contrast sensitivity at high-spatial frequencies, by contrast, has a longer developmental sequence, extending to around 6 years of age (see (Braddick & Atkinson, 2011; Norcia, 2011) for review).

Compared to the numerous studies of contrast sensitivity development, there have been fewer studies of the mechanisms that regulate contrast sensitivity. Following the work in animal models, the human literature has also used masking paradigms to study the regulation of contrast sensitivity, also known as contrast gain control. In the first study of this kind (Morrone & Burr, 1986) measured VEP amplitude as a function of contrast for low spatial frequency gratings that were masked by a second grating either of the same or orthogonal orientation. By presenting the test and mask gratings at different temporal frequencies, they were able to isolate the response to the test using spectral analysis, even during the presentation of the masker. They found that parallel maskers shifted the adult contrast response function rightward on the (log) contrast axis (contrast-gain control) but that an orthogonal masker changed the response slope (response-gain control). In infants, orthogonal maskers had no effect until 6 months of age, but parallel maskers did, starting as early as 20 days of age and increasing thereafter. A later study using similar methods found contrast gain effects for both parallel and orthogonal maskers in adults, with parallel maskers producing a larger rightward shift (Candy, Skoczenski, & Norcia, 2001). Cross-orientation maskers elevated contrast threshold by a constant factor of ~2. Contrast thresholds measured under the influence of the masker tracked the developmental change in threshold without the mask. By contrast, the magnitude of the threshold elevation created by the parallel masker increased systematically over the same age range. It is not clear why the two studies yielded different results. Differences in stimulus conditions were present as well as in the number of participants: Morrone and Burr reported data from 3 adults and longitudinal data from 3 infants, while Candy et al. showed data from 8 adults and 45 infants studied cross-sectionally and sampling biases may have played a role in the different results. In another study of VEP contrast masking (Skoczenski & Norcia, 1998) dynamic random noise maskers which are spatially broadband and un-oriented also produced contrast gain effects in both adults and in infants as young as 6 *wks* of age. In that study masked thresholds also paralleled unmasked thresholds by a constant factor, suggesting that contrast sensitivity rather than gain control processes were dominating the developmental trend.

Contrast masking in the adult psychophysical literature has traditionally been studied through its effects on contrast detection thresholds (Legge & Foley, 1980) and the emphasis of the Candy et al. and Skoczenski and Norcia studies was the effect of maskers on contrast thresholds as estimated by the VEP. Given that masking also affects the supra-threshold response function, we wished to study the late developmental phase of contrast sensitivity regulation using both threshold elevation and supra-threshold response function measures.

Prior work in animal systems (Albrecht & Geisler, 1991; Carandini et al., 1997; Heeger, 1992) and human (Brouwer & Heeger, 2011; Busse, Wade, & Carandini, 2009; Candy et al., 2001; Ross & Speed, 1991) has modeled contrast masking/gain control within a framework known as the normalization model (see (Carandini & Heeger, 2012) for review). Within this framework, the activity of cells tuned to a given spatial and temporal frequency combination is "normalized" by dividing their activity by the pooled sum over recent time and nearby spatial locations. The functional form of the output of the normalization model is sigmoidal with respect to stimulus contrast, saturating at higher input levels. Sigmoidal non-linearities have long been used to model psychophysical threshold masking (Legge & Foley, 1980). In our previous work in infants (Candy et al., 2001) and adults, (Tsai, Norcia, Ales, & Wade, 2011; Tsai, Wade, & Norcia, 2012a), we have used this framework to describe masking in the VEP. Here we test alternative versions of this model, one expressing contrast-gain effects and the other response-gain effects in school-age children and adults as a means of characterizing the late phases of development of this critical regulatory process.

2. Methods

2.1. Observers

Thirty-six typically developing children with normal or corrected to normal visual acuity, divided into two equal-sized age groups, participated. The first group consisted of eighteen 5–11 year-olds (8 female) and the second group comprised eighteen 12–17 year-olds (8 female). This division of ages corresponds roughly to the age of puberty. We also recorded from a group of 10 adult participants (4 female, average age 42 years). All the participants had normal or corrected to normal vision and did not have a history of neurological or psychiatric problems. We obtained written informed consent from all participants and one of their parents prior to the experiment in accordance with procedures approved by the Institutional Review Board of Stanford University. When the participant was a minor, assent was obtained from the child using a simplified version of the consent form that was signed by the child, with the parent signing the full consent form on behalf of the child.

2.2. Stimuli

We recorded Steady-State Visual Evoked Potentials (SSVEPs) in response to random checkerboard patterns presented on a contrast linearized CRT (HP1320) at a resolution of 800 × 600 pixels, a 72 Hz vertical refresh rate, and a mean luminance of 50.31 cd/m^2. The stimulus area was 37 by 28 deg when seen at a viewing distance of 70 cm.

To study both masked and unmasked contrast response functions, we used a two-frequency SSVEP paradigm in which one frequency tag (5.14 Hz) was assigned to a variable contrast test pattern and the other frequency tag (7.2 Hz) was assigned to a fixed-contrast masking pattern (Tsai et al., 2012a). The test and masking patterns consisted of random checkerboard patterns with two different luminance levels (binary noise; check size of 13 by 13 arc min). In the test condition, one of the patterns was presented alone and in the masking conditions two distinct patterns were superimposed.

Because the test and masker were tagged with different temporal frequencies, they were separable by Fourier analysis (Regan & Cartwright, 1970; Regan & Heron, 1969).

The protocol comprised three conditions: in the first condition, the variable contrast test was presented without a mask (unmasked condition). In the second condition a fixed 12% contrast masker was added to the test stimulus (12% mask condition) and in the third condition, a 40% contrast masker was used (40% mask condition). In the both masked and unmasked conditions, the test