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Behavioral measurement of temporal contrast sensitivity development in macaque monkeys (*Macaca nemestrina*)

Kara A. Stavros, Lynne Kiorpes *

Center for Neural Science, New York University, Room 809, 4 Washington Place, NY 10003, USA

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Abstract

We measured the developmental time course for temporal contrast sensitivity in macaque monkeys. The animals, aged 5 weeks to 4 years, detected an unpatterned field of light sinusoidally modulated over time at frequencies ranging from 1 to 40 Hz. Young infants showed reduced sensitivity for all frequencies, and a reduced range of detectable frequencies. Sensitivity to high and low frequencies developed at different rates, but the shape of the temporal contrast sensitivity function did not change significantly with age. Temporal contrast sensitivity matures earlier than spatial contrast sensitivity. The development of high, but not low, frequency sensitivity may be limited by maturation of the magnocellular pathway.

Keywords: Temporal vision; Visual development; Macaque monkey; Temporal contrast sensitivity; Magnocellular pathway

1. Introduction

Vision is immature at birth in primates and develops over some months or years thereafter. While much is known about the development of spatial vision (see Daw, 1995; Teller, 1997), comparatively little is known of the developmental time course for temporal vision.

A broad descriptor of temporal visual sensitivity is provided by the temporal contrast sensitivity function (tCSF), which relates the observer's contrast sensitivity to the temporal frequency of the stimulus (De Lange, 1958, 1952). The adult human tCSF is well characterized as band-pass in shape, with a peak at intermediate temporal frequencies. There is a gradual fall off at low temporal frequencies and a steep fall off at higher temporal frequencies to the high frequency cut-off, known as the critical flicker frequency (CFF). Many parameters have been shown to influence the shape of the tCSF (see De Lange, 1958; Kelly, 1971, 1972; Merigan, 1980; Snowden, Hess, & Waugh, 1995).

Few studies have investigated temporal contrast sensitivity development in human infants, and the existing data are conflicting. Initially, the CFF was measured in attempt to characterize the development of temporal vision (Horsten & Winkelman, 1964; Regal, 1981; see also Banks, 1983). Regal (1981) made direct, behavioral measurements of high frequency flicker sensitivity in 1, 2, and 3 month-olds and found that CFF approaches adult levels as early as age 3 months. Subsequent studies have estimated the CFF by extrapolation rather than by direct measurement. In these studies, CFF was estimated by extrapolation from measured sensitivity to lower frequency flicker or from modulation of drifting or counter-phase low spatial frequency gratings. Dobkins and Teller (1996) tested 3 month old infants using moving gratings of 0.25 cycles/degree (c/deg) at a range of temporal frequencies; they obtained an extrapolated CFF close to Regal's findings. However, a follow-up study of 3 and 4 month olds showed temporal resolution (in this case measured by the point at which the curve falls to one-half maximum) of roughly 10 Hz lower than adults tested under similar conditions (Dobkins, Anderson, & Lia, 1999). Several other studies used uniform field flicker at a range of temporal frequencies to compute

* Corresponding author. Fax: +1 212 995 4183.
E-mail address: lynne@cns.nyu.edu (L. Kiorpes).

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extrapolated CFFs for infants as old as 4 months and found the values to be considerably immature compared to adults (Hartmann & Banks, 1992; Rasengane, Allen, & Manny, 1997). While it is difficult to make direct comparisons across studies due to the different parameters and methods employed, Regal's (1981) direct measurement of CFF stands alone in showing very early development of temporal vision.

Several studies measured contrast sensitivity for temporal modulation over a range of frequencies below the CFF to study tCSF development. In spite of wide differences in stimuli, they have uniformly found substantial immaturities in overall sensitivity for low (1–2 Hz) and intermediate (5–10 Hz) temporal frequencies in infants as old as 8 months (Dobkins et al., 1999; Hartmann & Banks, 1992; Rasengane et al., 1997; Swanson & Birch, 1990; Teller, Lindsey, Mar, Succop, & Mahal, 1992). Furthermore, data from some of these studies suggest that sensitivity to high temporal frequencies matures at a different rate than sensitivity to low temporal frequencies implying that the tCSF changes shape during development (Hartmann & Banks, 1992; Rasengane et al., 1997; Teller et al., 1992). Interestingly, the notion that the tCSF changes shape was not borne out; Dobkins et al. (1999) found that the shape of the tCSF in 3- to 4-month-old infants was similar to adults, as was peak temporal frequency. However, the idea that sensitivity to high temporal frequencies matures at a different rate than low temporal frequencies was bolstered by a study of tCSF in children, ages 4–7 years (Ellemberg, Lewis, Liu, & Maurer, 1999). They found that sensitivity to low temporal frequencies does not reach maturity until age 7, while sensitivity to higher temporal frequencies (including CFF) was mature in all age groups tested. Taken together, the human infant temporal contrast sensitivity studies suggest a differential development of high and low temporal frequencies and a considerable increase in temporal contrast sensitivity over the course of development. However, it is difficult to draw clear conclusions since there is wide variation in methodology across studies and there are no data from children between the ages of 8 months and 4 years.

We undertook to clarify the developmental profile for temporal vision by measuring full tCSFs over the complete course of maturation in an animal model. The macaque monkey provides an excellent model for the human visual system and monkeys produce quantitative, reliable data at virtually any age throughout development. Data describing the tCSF of the adult monkey have been long established (Harwerth, Smith, Boltz, Crawford, & von Noorden, 1983; Merigan, 1980; Merigan, Pasternak, & Zehl, 1981). These studies demonstrate that, in general, the adult monkey tCSF is similar in shape to the human tCSF, but humans are slightly more sensitive at intermediate and low temporal frequencies while monkeys typically have higher CFFs. No prior studies of temporal visual development have been published for infant monkeys.

In the study described here, tCSFs were obtained from fourteen monkeys at different stages of development to track the maturation of temporal contrast sensitivity for unpatterned sinusoidal flicker. We considered three important questions concerning temporal contrast sensitivity development. First, does the range of temporal resolution expand over development? Second, at what age does temporal contrast sensitivity reach maturity? And third, does development of sensitivity to high and low temporal frequencies proceed at different rates, i.e., does the curve change shape? We also compared the rate of development for temporal and spatial contrast sensitivity. We found temporal contrast sensitivity to be fully mature by approximately 20 weeks, following small increases in temporal frequency range and substantial increases in overall sensitivity. Further, we found that sensitivity to high temporal frequencies reaches maturity more rapidly than sensitivity to lower temporal frequencies. However, it appears that the tCSF does not change shape significantly during maturation. We also found that temporal vision develops more quickly than spatial vision. Lastly, comparison of our behavioral data with studies examining the development of temporal responsiveness in single neurons suggests that at least some of temporal development is limited at or before the level of the LGN.

2. Materials and methods

2.1. Subjects

Subjects in this study were fourteen visually normal pigtailed monkeys (*Macaca nemestrina*) ranging in age from 5 weeks to 230 weeks. All animals were born at the Washington National Primate Research Center and hand-reared at the New York University Visual Neuroscience Laboratory. The monkeys were provided with a normal visual environment, which was enriched with a variety of appropriate visual and tactile stimuli. Four monkeys were tested longitudinally from infancy, 2 were tested at multiple ages from 6 months postnatal, and 8 were tested at only one age (range: 16 weeks to 227 weeks). All testing was conducted in accordance with the *NIH Guide for Care and Use of Laboratory Animals* and approved New York University IACUC protocols.

2.2. Stimulus

Stimuli were large Gaussian-windowed patches of spatially unpatterned light displayed on a computer screen in a dark room. We chose a large stimulus size and a Gaussian profile to minimize edge effects (Kelly, 1972). The stimuli were generated on a 21 inch Eizo FlexScan FX-E8 color display monitor (frame rate = 160 Hz) driven by a Dell Optiflex GX1 computer via a VSG2/3 graphics card (Cambridge Research Systems). The standard viewing distance for all monkeys was 50 cm, at which distance the usable monitor area subtended 39 deg (w) × 27 deg (h). Stimuli subtended 17 deg of visual angle and appeared to the left or right of the screen center at an eccentricity of 11 deg. To obtain temporal contrast sensitivity measurements, the luminance of the stimulus was modulated sinusoidally over time about its mean (56 cd/m^2). The surround had constant mean luminance which was equal to the time-average luminance of the stimulus (cf. De Lange, 1958). We tested the following temporal frequencies at all ages: 1, 2, 4, 8, 16, 25, and 40 Hz. The stimulus ramped on and stayed on for 500 ms for adult monkeys, after which time the animals were free to respond. Infants were given up to 1000 ms to respond (see below).