

Visual acuity development coincides with the sensitive period in kittens

At about ten days of age when a kitten's eyes open, synaptic connections of its visual system are partly laid down¹. They are completely developed during the sensitive period² which lasts from about three weeks of age to three months. During this period of plasticity the formation and modification of synaptic connections respond to features in the visual environment³⁻⁶. Both the original and subsequently developed connections may be disrupted or modified by environmental factors during the sensitive or critical period with a sensitivity that peaks at about the fourth week and gradually drops off².

Conventional (psychophysical) visual acuity as well as its electrophysiological acuity correlate, obtained by pattern-dependent visual evoked potentials, must also develop in the kitten as a result of the organisation of synaptic connections. (Visual evoked potential acuity measurements are based on electrical processing in the visual cortex, although it is possible that they may reflect retinal and geniculate processing resolution before cortical processing takes place.) Our goal was to measure visual acuity in cats and kittens of various ages to determine the time course of its development.

Visual evoked potential acuity measurements were made on nine kittens and three adult cats, all raised in a normal visual environment. The data were obtained from the two eyes separately in each of four kittens and in one eye in the rest of the kittens and cats, providing fifteen data points in all. A horizontal rather than longitudinal time study was dictated because stable electrodes were difficult to maintain through the thin, growing skull of the kittens. Following the method of Rose *et al.*⁷, stainless steel screw electrodes were positioned just through the skull over the visual cortex and, with dental acrylic cement, were encased in a small electric connector on the head. The implantation of electrodes yielded excellent potentials with a much better signal to noise ratio than did surface electrodes.

The responses were evoked by the virtually instantaneous reversal of the light and dark stripes of a bar grating pattern by an optical electromechanical shaker. A constant temporal frequency of 0.5 Hz was used with a variable bar width (spatial frequency). During recordings the animals were quiescent under general anaesthesia (sodium pentobarbital) and a contact lens protected the optical quality of the cornea. It is clear that the optical quality of the eye of the very young kitten is inferior to that of the adult. But on the basis of ophthalmoscopic observation we feel that it is unlikely that optical factors limit the acuity determined for the younger animals. The eye was aligned to the screen by finding the optic disc ophthalmoscopically and projecting it on to the screen. Retinoscopy and trial lenses provided an optical correction to the screen at 57 cm which covered a 40° visual angle. The target had 80% contrast and a luminance of 24 cd m⁻².

For each size or spatial frequency of grating, 100 responses were recorded and averaged on a PAR Waveform Educator to provide a good signal to noise ratio (Fig. 1). Measurements were begun at 23 days of age, well after the hyaloid artery disappeared and the optical media were clear. The amplitude of the evoked response was found to be a function of the spatial frequency of the pattern, confirming Berkley and Watkins⁸. Visual acuity was taken as the highest spatial frequency for which a clear electrical response was present. Spatial frequency thresholds for each animal were plotted on a log-log scale as a function of age (Fig. 2, solid curve).

The points on the curve are, in principle, slightly above threshold because a clear though minimum response was used as the criterion. At the next higher step of spatial frequency no response could be observed, so the exact threshold cannot be

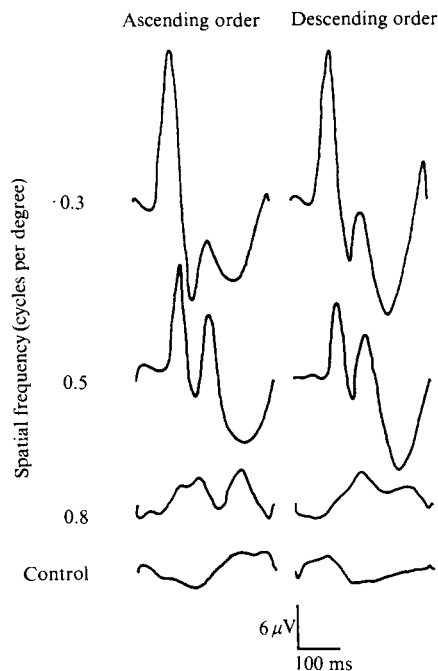


Fig. 1 Pattern evoked potentials from stimulation of the right eye of a 31-d-old kitten. Measurements were recorded for different fineness of bar gratings (spatial frequencies) in ascending and then descending order. The control was a static projection of the 0.3 cycles per degree pattern.

above these points which are represented by the dashed curve of Fig. 2. This curve is at or slightly below threshold and is the limit of the maximum possible error in the minimum threshold as determined by this method.

Grating resolution of the adult cats fell between 3 and 5 cycles per degree which is similar to that found by Berkley and Watkins⁸ and by Campbell *et al.*⁹ using related evoked potential methods, and by Muir and Mitchell¹⁰ using a standard psychophysical method. Recently Blake *et al.*¹¹ using conditioned suppression were able to approach 6 cycles per degree. Wässle¹²

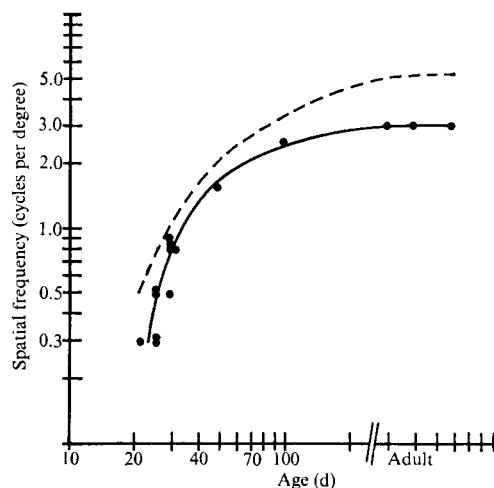


Fig. 2 The highest spatial frequency for which an evoked potential was present is graphed as a function of age (closed circles). A curve has been fitted by eye to these points (solid line). The dashed line joins the next higher spatial frequencies for which no pattern evoked potentials were present and is a measure of the maximum error. Age scale for adult cats is in yr.

found a comparable value for the optical upper spatial frequency cut-off using two parallel slits for the cat's eye, calculated at 4 to 5 arcmin or 6 cycles per degree. Pure optical values would be expected to be the same or higher than the psychophysical acuity value of 3 to 5 cycles per degree. These values seem low when compared with those of the human eye; the cat's optical system, however, is poorer¹⁰ and its retina lacks a fovea centralis.

It is clear from the trend of the curve that from 23 days of age, development of visual acuity in the cat is exceedingly rapid, and is virtually complete by 100 d. At 23 d of age acuity was only 0.3 cycles per degree or 20/2000 Snellen. Ten days later the acuity had improved to 1 cycle per degree or 20/600, an enormous increase. Between 33 d and 100 d the acuity approached the adult level of 3 cycles per degree, or 20/200.

The optical media may become slightly clearer during the third to sixth week which could make a curve representing synaptic development slightly less steep. Fig. 2 may also be described as follows: It "... begins suddenly near the start of the fourth week, at about the time a kitten begins to use its eyes, and persists until some time between the sixth and eighth weeks; it then begins to decline, disappearing ultimately around the end of the third month." This is Hubel and Wiesel's description² of the sensitive period for changes in ocular dominance which fit our data. Their descriptive data have been plotted by Blakemore¹³. While other functions of the visual system may have somewhat different sensitive periods, it seems likely that all other functions fit within the limits of that described above for ocular dominance.

Because the normal development of acuity takes place during the sensitive period, our findings support the hypothesis that this development may be used as a measure of the visual sensitive period. A similar but non-invasive method (that is, using electrodes on the skin rather than on the brain) can be used to investigate the visual development of the human infant in order to study the human visual sensitive period and its time course.

This work was supported by a fellowship from Fight-for-Sight, Inc. New York City to D.N.F., the US National Institutes of Health, and the US National Science Foundation.

DONALD N. FREEMAN
ELWIN MARG

*School of Optometry,
University of California,
Berkeley, California 94720*

Received January 3; revised February 24, 1975.

- ¹ Hubel, D. H., and Wiesel, T. N., *J. Neurophysiol.*, **26**, 994-1002 (1963).
- ² Hubel, D. H., and Wiesel, T. N., *J. Physiol., Lond.*, **206**, 419-436 (1970).
- ³ Hirsch, H. V. B., and Spinelli, D. N., *Science*, **168**, 869-871 (1970).
- ⁴ Blakemore, C., and Cooper, G., *Nature*, **223**, 477-478 (1970).
- ⁵ Pettigrew, J. D., and Barlow, H. B., *J. Physiol., Lond.*, **218**, 98-100P (1971).
- ⁶ Blakemore, C., and Mitchell, D. E., *Nature*, **24**, 467-468 (1973).
- ⁷ Rose, G. H., Gruneau, S., and Spencer, J. W., *Electroenceph. clin. Neurophysiol.*, **33**, 141-158 (1972).
- ⁸ Berkley, M. A., and Watkins, D. W., *Vision Res.*, **13**, 403-415 (1973).
- ⁹ Campbell, F. W., Maffei, L., and Piccolino, M., *J. Physiol., Lond.*, **229**, 719-731 (1973).
- ¹⁰ Muir, D. W., and Mitchell, D. E., *Science*, **180**, 420-422 (1973).
- ¹¹ Blake, R. B., Cool, S. J., and Crawford, M. L. J., *Vision Res.*, **14**, 1211-1217 (1974).
- ¹² Wässle, H., *Vision Res.*, **11**, 995-1006 (1971).
- ¹³ Blakemore, C., *Br. med. Bull.*, **30**, 152-157 (1974).