The high cost is primarily due to the cost of mucus production, which alone is greater than the total cost of movement for a mammal or reptile of similar weight, a fact which may be useful in examining the evolutionary ecology of slugs and other animals with similar locomotory systems. It seems likely that the high cost of movement has affected the "lifestyle" of these animals, for example, by limiting the distance over which it is profitable to crawl in search of mates or food.

MARK DENNY*

Department of Zoology,
University of British Columbia,
Vancouver, Canada

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5. The animal was housed in an airtight box containing a CO$_2$ absorbent. As the animal respires, CO$_2$ produced is absorbed and the pressure in the test chamber decreases relative to a reference chamber. The pressure difference bends a diaphragm separating the two chambers and changes the orientation of a mirror mounted on the diaphragm, which in turn deflects a light beam away from an electronic photodetector, causing a relay to close and current to be passed through an electrolysis cell in the test chamber. The electrolysis of the CuSO$_4$ solution in the cell releases O$_2$ into the chamber and completes the feedback loop. A chart recorder records the amperage passed through the cell and provides a means for calculating a time record of O$_2$ consumption. Both chambers are submerged in a constant temperature bath at 19.5 ± 0.01°C. Consumption of 0.01 ml of O$_2$ can be detected. The test chamber is supported by a vertical central beam which is bent as the slug crawls. Strain gauges, glued to the beam, measure this bending along orthogonal axes, and the output from the gauges is recorded on a two-channel chart recorder, providing a continuous record of the horizontal location of the slug's center of mass. The test chamber is 25 cm wide by 25 cm long by 1.9 cm high so that, while vertical movements are not measured, these are small compared to horizontal movements. From the strain gauge record the total distance moved and the speed of movement are calculated.
6. The respiratory quotient was measured by comparing the apparent rate of O$_2$ comsumption with and without CO$_2$ absorbant in the respirometer. It is assumed that the animal uses only carbohydrate in powering locomotion, and a value of 20.9 J per milliliter of O$_2$ (at STP) is used [C. L. Prosser and F. A. Brown, *Comparative Animal Physiology* (Saunders, Philadelphia, 1961)].
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12. I thank J. M. Gosline and S. K. Denny for their advice and support. Funds for this study were provided by NRC grant 67-6934 (to J.M.G.).

* Present address: Department of Zoology, University of Washington, Seattle 98195

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Development of Contrast Sensitivity in Infant *Macaca nemestrina* Monkeys

Abstract. *During an infant monkey's first 28 postnatal weeks, the visual contrast sensitivity function develops its characteristic adult form. Contrast sensitivity is depressed relative to that of the adult for all spatial frequencies during the early postnatal weeks. Absolute sensitivity to frequencies below 5 cycles per degree approaches adult levels by 20 weeks after birth, whereas sensitivity to fine spatial detail continues to develop through 28 weeks. The results imply that the development of primate spatial vision is more complex than just an improvement in the ability to resolve acuity gratings.*

Primate visual acuity is immature at birth. Acuity improves gradually during the first six or more months after birth in human infants and during the first six or more weeks in macaque monkey infants. If the monkey time axis is expanded by about a factor of 4, the two species coincide closely over the early postnatal weeks (*1*). This developmental similarity, in combination with the established similarity of visual capacities of adults of the two species (*2*), supports the conclusion that the macaque monkey provides a good animal model for the development of human spatial vision.

Visual acuity provides information only about sensitivity to very fine, high-contrast spatial detail. The spatial contrast sensitivity function (CSF) provides information about visual sensitivity over the entire spatial frequency spectrum, including the acuity point (*3*). Thus, the study of CSF's during development provides a more complete description of the emergence of spatial vision. Through the use of nonoperant techniques (*4*), CSF's have been obtained from human infants between 1 and 3 months after birth. To our knowledge, operant testing methods, used extensively with nonhuman primates in other contexts, have not been used to obtain CSF's from infants.

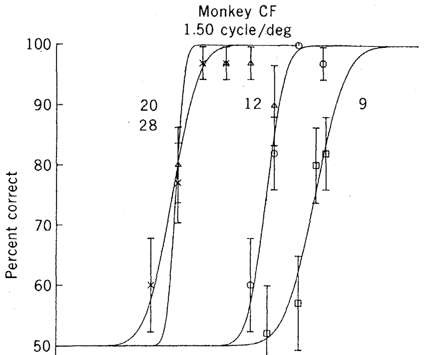

Fig. 1. Psychometric functions generated by infant CF 9 (□), 12 (○), 20 (△) and 28 (×) weeks after birth. Each data point was determined from a total of 40 trials with one contrast of a 1.5 cycle/deg grating. The error bars plotted around each point are ±1 standard error of the mean of the binomial distribution. A cumulative normal curve has been fit to each data set using a least-squares criterion. Each point was weighted according to its binomial statistics. The contrast value where the best-fit curve crosses the 75 percent correct level is used as an estimate of threshold contrast.

We have studied two infant *Macaca nemestrina* monkeys longitudinally by means of a specialized operant testing method. We found that contrast sensitivity increased with age at all spatial frequencies, but sensitivities to different spatial frequencies improved according to different time-courses. Sensitivity to low spatial frequencies reached an asymptote near adult levels first, whereas sensitivity to higher frequencies continued to improve over a longer postnatal period. This resulted in changes with age in the peak spatial frequency as well as in the high-frequency cutoff of the CSF.

We obtained contrast sensitivity measures from our infant monkeys in a two-alternative forced-choice psychophysical experiment. A spatial sinusoidal grating was generated on one of two cathode-ray tube (CRT) screens. The sinusoidal nature of the grating, its spatial frequency and contrast, and the position of the grating (on the left or on the right CRT) were controlled by computer (*5*). The spatial frequencies ranged from 0.8 to 25 cycle/deg, with each display containing six or more cycles of the grating.

The infant monkeys entered a strict shaping routine about 1 week after birth, during which they were eventually trained to discriminate between a sinusoidal grating displayed on one CRT and a homogeneous field of matched space-averaged luminance displayed on the other. The mean luminance was 27 candles per square meter. The monkeys were trained and tested in their home cages according to a face mask technique (*6*). The face mask consisted of a piece of plastic molded into the shape of a monkey's face, with eye holes for viewing the stimuli and a mouth hole for receiving reinforcement. Two grab bars, right and left, were located within easy reach through an armhole below the mask.

The monkey was rewarded with a small amount of milk formula when he correctly identified the position of the stimulus by pulling the appropriate grab bar. An incorrect response was followed by a time out of 10 to 20 seconds signaled by a tone. The face mask allowed us to control viewing distance precisely and, therefore, to specify the spatial frequency of the grating.

Psychometric functions generated by infant CF, with a 1.5 cycle/deg grating are shown in Fig. 1. Between 9 and 12, and again between 12 and 20 weeks, the threshold shifted to a lower contrast. The curves obtained at 20 and 28 weeks are nearly superimposed, with thresholds near 1 percent contrast. These curves, typical of data obtained from our two infant monkeys, indicate that the monkeys' sensitivity to this low spatial frequency reached an asymptote before 20 weeks of age.

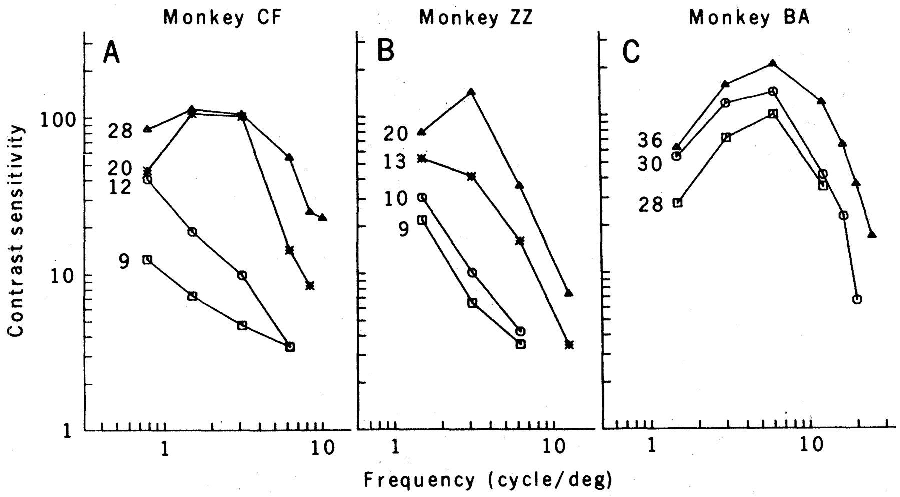

Fig. 2. Contrast sensitivity functions for infants CF and ZZ and for control monkey BA. Contrast sensitivity (reciprocal of threshold contrast) is plotted as a function of the spatial frequency of a grating (in cycles per degree of visual angle) on log-log coordinates. The infant's age in weeks at which each CSF was measured is indicated next to each curve.

We have obtained similar data at a number of spatial frequencies, and the trend of decreasing contrast threshold (increasing contrast sensitivity) with increasing postnatal age, is apparent. However, the time course of contrast sensitivity development is not the same for all spatial frequencies (Fig. 2, A and B). The CSF's measured at 9 and 12 weeks in monkey CF show highest contrast sensitivity at the lowest frequency tested (0.8 cycle/deg) (*7*). A peak in the region near 3 cycle/deg first appeared at 20 weeks. By this age, contrast sensitivity to frequencies between 0.8 and 3.1 cycle/deg was near adult levels, and the low-frequency portion of the CSF resembled that of an adult. Between 20 and 28 weeks, the major change was the increased sensitivity to frequencies 6.2 cycle/deg and higher. The CSF at 28 weeks, with peak sensitivity between 1.5 and 3 cycle/deg, did not yet resemble earlier reports of adult macaque CSF's (*2*) or data from older macaques in our laboratory (Fig. 2C), all of which showed peak contrast sensitivity near 5 or 6 cycle/deg.

Similar observations can be made from infant ZZ's data (Fig. 2B), although CSF's were obtained only through 20 weeks of age, and the lowest frequency tested was 1.5 cycle/deg. The data between 9 and 20 weeks in the two infants coincide well with respect to the changes in the CSF with age. The earlier ages show highest sensitivity at the lowest frequency tested. A peak near 3 cycle/deg is first seen at 20 weeks.

As we observed these changes in contrast sensitivity during development, we were concerned that the trends we measured might be influenced by practice. It is conceivable that the infants learned to respond to patterns of low spatial frequency more easily than to those of high frequency. To sort out training from developmental changes, we delayed the onset of training for a control monkey until 25 weeks of age. The first CSF was obtained from this monkey after 3 weeks of training (Fig. 2C) and shows a peak near 6 cycle/deg. The next two functions measured, representing a total of eight more weeks of practice, showed a general improvement in sensitivity to all spatial frequencies, but no obvious changes in position of the peak. None of the CSF's obtained from monkey BA through 50 weeks were appreciably different from the 36-week function shown. These results from the control monkey can be compared with the infant CSF's (Fig. 2, A and B). The changes in the infants' relative sensitivities to different frequencies do not appear to be mimicked by a training or practice effect.

The anatomical and physiological changes (*8*) as well as changes in optical factors (*9*) that might be responsible for the observed behavioral effects are as yet unknown. The development of the CSF could reflect the activity of a single mechanism that changes its properties during development. An example would be a center-surround receptive field that changes its size or the amount of center-surround antagonism. Alternatively, the developmental changes observed might result from an envelope or combination of different spatial mechanisms whose sensitivities develop with different time courses. The low-frequency mechanisms would reach adult levels of sensitivity early, whereas middle- and high-frequency mechanisms continued to mature. In either case, the underlying mechanism or mechanisms continue to develop for the first 28 weeks or more after birth in infant macaque monkeys.

If, as has been suggested on the basis of acuity data, a week of visual development in a macaque monkey infant is about equal to a month of visual development in a human infant (*1*), our contrast sensitivity data suggest that continuing changes will be found in the human CSF throughout the first 28 months of postnatal development. Such continuing changes in acuity have been reported recently in children through 3 years of age (*10*). It will be interesting to see if behavioral, physiological, and anatomical changes continue to be reported in monkey and human visual systems over such extended postnatal periods.

RONALD G. BOOTHE,
RICK A. WILLIAMS
LYNNE KIORPES
DAVIDA Y. TELLER
Departments of Psychology and
Physiology and Biophysics, Child
Development and Mental Retardation
Center, and *Regional Primate*
Research Center, University of
Washington, Seattle 98195

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2. R. L. DeValois, H. Morgan, D. M. Snodderly, *ibid.* **14**, 75 (1974).
3. For a sinusoidally modulated grating of a particular spatial frequency (defined as the spatial periodicity of the grating in cycles per degree), the contrast [defined as $(L_{\max}-L_{\min}) / (L_{\max}+L_{\min})$ where L is luminance] that can just be detected is called the threshold contrast. Contrast sensitivity is defined as the reciprocal of threshold contrast. A plot of contrast sensitivity as a function of the spatial frequency of the grating stimulus is called a contrast sensitivity function. In both adult humans and adult macaque monkeys,

the CSF, measured behaviorally, exhibits a characteristic shape (for example, Fig. 2C). The peak of the CSF refers to the spatial frequency where the highest contrast sensitivity occurs. At lower frequencies, decreasing contrast sensitivity results in a low-frequence falloff. At higher frequencies, contrast sensitivity also decreases. The frequency at which high frequency sensitivity falls off to a value of 1.0 is referred to as the cutoff spatial frequency. The cutoff frequency represents the limit of resolution of a 100 percent contrast sinusoidal grating; its value is closely related to grating acuity, which is usually measured with high-contrast square-wave gratings.

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5. Two problems encountered when using CRT display systems are (i) the relationship between input voltage and output luminance is not linear, and (ii) the spatial frequency response function is not flat over the frequency range of interest. Our computer-controlled display system was calibrated and then programmed to compensate for both the nonlinearity and the frequency response.
6. For a general discussion of the development of the face mask technique for studying perception and learning in infant monkeys, see G. P. Sackett, R. Tripp, C. Milbrath, J. Gluck and H. Pick [*Behav. Res. Methods Instrum.* **3**, 233 (1971)]. For an application of the method to visual psychophysics experiments in infant monkeys, see R. Boothe, D. Y. Teller, and G. P. Sackett [*Vision Res.* **15**, 1187 (1975)].
7. There may, of course, be a low-frequency falloff below the range tested. Apparatus limitations prevented us from presenting gratings of lower frequency with an adequate number of cycles. We have recently modified our apparatus so we can present lower spatial frequencies with sufficient numbers of cycles. Preliminary indications from a single infant are that frequencies as low as 0.2 to 0.4 cycle/deg must be used before a low-frequency turndown can be detected in young infant monkeys.
8. Anatomical changes take place in the macaque monkey visual system during the same postnatal period during which we have found the behavioral CSF to be changing. The retina changes postnatally in density, size, shape, and in the ultrastructure of foveal cones [T. Samorajski, J. R. Keefe, J. M. Ordy, *Vision Res.* **5**, 639 (1965); A. Hendrickson and C. Kupfer, *Invest. Ophthalmol.* **15**, 746 (1976)]. In the striate cortex, there are changes in dendritic arborizations and in the numbers of presumed connections between neurons [J. S. Lund, R. G. Boothe, R. D. Lund, *J. Comp. Neurol.* **176**, 149 (1977); R. G. Boothe, W. T. Greenough, J. S. Lund, K. Wrege, *ibid.* **186**, 473 (1979)].
9. Clarity of the optics, eye size, and accommodative response might all play a role in the development of the CSF, but all of these factors are probably minor in relation to the size of the effects found. The optics of the infant monkey eye are clear at birth by ophthalmic examination. Measurements of the optical line spread function reveal that optical quality is very good within days after birth and resembles that of the adult by 2 months (R. A. Williams and R. G. Boothe, in preparation). An increase in axial length between 4 and 20 weeks of age increases retinal image size by a factor of about 1.14, a magnification much too small to account for the observed changes in the CSF. It is not known whether infant monkeys can accurately accommodate to our stimuli. However, the data shown in Fig. 2, A and B, were obtained at two different viewing distances, 60 and 120 cm respectively. The similarity of the two sets of data leads us to believe that accommodation also contributes little to the developmental trends shown.
10. L. Mayer and V. Dobson, in preparation.
11. Supported in part by NSF grant BNS 75-01451 to D.Y.T., NEI grant 1 RO1 EY02510 to R.G.B., NIH grant RR 00166 to the Regional Primate Research Center, and NICHHD grant 02274 to the Washington Regional Child Development and Mental Retardation Center. We thank G. Ruppenthal and the staff of the Infant Primate Research Facility for their assistance and cooperation in caring for our infant monkeys. We thank V. Dobson and S. Buck for commenting on earlier versions of the manuscript and M. Zachow for secretarial assistance. A preliminary report of this work was presented at the annual meeting of the Association for Research in Vision and Ophthalmology, Sarasota, Fla., 30 April to 4 May 1979.

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Thermocline Temperature Differences and Realizable Energy

The report by McNichols *et al.* (*1*) seems too superficial in its treatment of a relatively simple analysis. My first objection is to applying Carnot efficiency calculations to the total system of heat exchangers and expansion engine. Strictly speaking, the Carnot analysis applies only to the expansion engine. The gross temperature difference must then be allocated between the heat exchangers and the expansion engine.

The TRW Systems Group deals in some detail with this matter in their Ocean Thermal Energy Conversion (OTEC) report (*2*). The OTEC temperature levels and temperature differences are of the same general order of magnitude as those used by McNichols *et al.* (OTEC temperature levels and temperature differences may be slightly higher). The allocation of the total temperature difference used by TRW is 50 percent to the heat engine and 50 percent to heat exchanger energy transfer. Two important considerations flow from this allocation. The first is that all of the gross energy carried by the warm water leaving the working-fluid boiler bypasses the generating unit entirely. Therefore, the energy actually transferred into the working fluid is already only a small portion of the gross energy originally available.

The second consideration is that the Carnot efficiency must be calculated for the temperature differences and levels associated with the expansion device. Only after the Carnot efficiency is calculated on the basis of a consideration of the appropriate data is it correct to apply the realization factor of 50 percent to the Carnot efficiency.

In short, the report by McNichols *et al.* fails to recognize that Carnot thermal efficiency is only a part of the entire analysis. The conversion of gross temperature difference to equivalent head, although mathematically correct, is essentially meaningless because energy quantity depends upon both head and flow quantity. When allowance is made for the fact that most of the gross heat quantity never reaches the conversion device and the appropriate temperature difference across the expansion engine is used, then the effective head is only on the order of one-tenth that shown in (*1*, p. 168). Clearly, an equivalent effective head of 16 m is not nearly as impressive as a potential head of 160 m. It is unfortunate that this fragmentary analysis did not include a consideration of the importance of relating the head to the correct flow quantity when discussing realizable energy quantities.

EMORY H. HALL
Bonneville Power Administration,
Post Office Box 3621,
Portland, Oregon 97208

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In their report on the use of the thermocline temperature differences in hydroelectric reservoirs, McNichols *et al.* (*1*) overstate the potential power output by a factor of $\gtrsim 8$. It is clear from their report that they consider only the use of the normal outflow of water (for if recirculation back into the reservoir is allowed, the system reduces to an Ocean Thermal Energy Conversion type concept with outputs limited only by solar input and system size). For such an application, the assumption of a value $\Delta T/T$, where T is absolute temperature, for Carnot efficiency is incorrect, since the heat source and sinks are finite. The hot and cold water flows approach one another in temperature so that the effective mean temperature difference is less than ΔT.

For a mass flow rate of m (in kilograms per second), of which a fraction α is at a temperature $T + \Delta T$ and $1 - \alpha$ is at T, the maximum (Carnot) mechanical power output P (in watts) is given by

$$P = mC[T + \alpha\Delta T - T^{1-\alpha}(T + \Delta T)^{\alpha}] \approx mC\Delta T \frac{\Delta T}{T}\alpha\frac{(1-\alpha)}{2} \text{ for } 0 \leq \frac{\Delta T}{T} << 1 \qquad (1)$$

where C (in joules per kilogram per kelvin) is the specific heat of water. The extra factor $\alpha(1 - \alpha)/2$ in Eq. 1, compared with equation 3 in McNichols *et al.*, leads to my statement above.

E. A. C. CROUCH
Department of Physics,
Harvard University,
Cambridge, Massachusetts 02138

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