Development of contour integration in macaque monkeys

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Abstract

Studies of visual development show that basic metrics of visual development such as spatial resolution develop over the first 6–9 months in monkeys and over the first 6 or so years in humans. However, more complex visual functions may develop over different, or more protracted, time courses. To address the question of whether global perceptual processing is linked to or otherwise dependent on the development of basic spatial vision, we studied the development of contour integration, a global perceptual task, in comparison to that of grating acuity in macaque monkeys. We find that contour integration develops substantially later than acuity. Contour integration begins to develop at 5–6 months, near the time that acuity development is complete and continues to mature well into the second postnatal year. We discuss this later development in terms poor central efficiency and consider the relevant anatomy and physiology of the developing visual system. We conclude that contour integration is not likely to be limited by the same mechanisms that are permissive to acuity development, and may instead reflect the emergence of function central to V1.

Keywords: Visual development, Contour integration, Monkey

Introduction

The sensitive period for vision is correlated with the duration of visual development (see Daw, 1998). The usual benchmark for visual development is the maturation of spatial resolution. In preverbal and animal subjects, resolution is typically measured by grating acuity rather than by letter acuity. When measured psychophysically, grating acuity develops to adult levels over the first 3-6 years after birth in humans (see Levi & Carkeet, 1993; Teller, 1997; Neu & Sireteanu, 1997; Ellemberg et al., 1999) and over the first 6-9 months in macaque monkeys (Boothe et al., 1988; Movshon & Kiorpes, 1988; Kiorpes, 1992). Other metrics of visual sensitivity reveal different time courses. For example, stereoacuity develops quite rapidly during the early postnatal weeks or months. Birch (1993; Birch et al., 1982) has documented abrupt onset of stereoacuity between about 4 and 6 months in human infants (see also, Brown & Miracle, 2003; Wattam-Bell, 2003). O'Dell and Boothe (1997) have shown a similar pattern of stereoacuity development in nonhuman primates, with an abrupt onset around 4-6weeks. However, in neither case is it completely clear when adult levels of stereoacuity are reached. Vernier acuity is relatively immature in newborns, in comparison to grating acuity (Shimojo & Held, 1987; Kiorpes, 1992; Zanker et al., 1992; Carkeet et al., 1997; Skoczenski & Norcia, 1999). In humans, the developmental time course is quite protracted and approaches adult performance levels between 5 and 6 years of age (Zanker et al., 1992; Levi & Carkeet, 1993; Carkeet et al., 1997) but may not be quite adult even at age 7 years (Carkeet et al., 1997). Spatial contrast sensitivity is adult-like by 7–8 years (Bradley & Freeman, 1982; Abramov et al., 1984; Hainline & Abramov, 1997; Ellemberg et al., 1999), while temporal contrast sensitivity is already mature at 4 years (Ellemberg et al., 1999). Some authors propose that remaining sensitivity differences between children and adults at age 8 may be due to nonvisual factors (Bradley & Freeman, 1982; Abramov et al., 1984). Taken together, it appears that all such basic spatial visual functions are adult-like or nearly so in humans by about 8 years and in monkeys by 9–12 months.

The question that follows naturally is, once basic visual functions are mature, are more global aspects of vision also mature? That is, can the child perform more complex visual tasks such as spatial integration and figure-ground segregation similarly to the adult or do these abilities mature independently or at later ages? Here there is a wide range of variation depending on the nature of the task. Recent studies by Kovács and colleagues in children suggest that perceptual organization skills mature substantially later than basic spatial acuity (Pennefather et al., 1999; Kovács et al., 1999; Kovács, 2000). They found that contour integration only becomes apparent at 3-4 years and continues to mature into the teenage years. On the other hand, sensitivity to illusory contours is apparent as early as 4 months after birth (Johnson & Aslin, 1998; Curran et al., 1999; Kavšek, 2002), and orientation-defined boundary detection is evident in infants as young as 3-4 months (Atkinson & Braddick, 1992). However, there is also evidence that certain texture segmentation abilities mature quite late, during childhood. The ability to discriminate a figure defined by orientation differences between figure and background is not present at

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such young ages and does not mature until 7–8 years (Sireteanu & Rieth, 1992; Rieth & Sireteanu, 1994) and in some cases until the late teen years. Identification of motion-defined form, in a letter identification task, also matures around age 7–8 (Giaschi & Regan, 1997). However, Snellen acuity (as measured using a letter chart) matures gradually up to age 9 or 10 (Giaschi & Regan, 1997). Finally, sensitivity to chromatic variation continues to fluctuate over the life span (Knoblauch et al., 2001). Thus the distinction among the early and late maturing tasks is not completely clear. Long developmental programs may suggest processing that depends on second-order cues, global perceptual organization, or other stimulus features, or perhaps cognitive factors. Different mechanisms may be involved in maturation of such tasks and they may have more extended critical periods than basic spatial vision.

To study directly critical periods in development and underlying neural mechanisms, it is necessary to study animal models. No data are available on the development of complex tasks such as texture segmentation or perceptual organization in nonhuman primates. Texture segmentation appears to develop relatively late in comparison to acuity in kittens as well as in humans (Wilkinson & Crotogino, 1995). It is reasonable to suppose that such integrative spatial abilities depend on the correlation and combination of information across space, and thus, may depend on higher level visual areas than does acuity, or they may await the development of more sophisticated intracortical circuitry.

To establish the relative developmental time courses, we studied the development of contour integration abilities in comparison to the development of grating acuity in individual macaque monkeys. The aim of the study was to assess whether global perceptual organization is limited by acuity development or develops independently of acuity. Evaluation of these functions in the monkey allows us to make quantitative comparisons across tasks, within subjects and over long age spans, and to eventually study directly important neural substrates. We used a task that is similar to one previously used in human psychophysics (Kovács, 1996; Pettet et al., 1998). The task required the detection of a feature (a circular contour) in the presence of background noise. Detection of the contour requires perceptual linking of the elements in the ring in the presence of noise elements. This is considered to be a "global" task as the feature linking cannot be solved on the basis of detection of the local features alone. Our results show that maturation of contour integration begins well after that of acuity and continues beyond the age at which acuity development ends. Some of these data have been presented in abstract form (Kiorpes et al., 2000, 2001).

Materials and methods

Subjects

Ten visually normal *Macaca nemestrina* monkeys were subjects in this study. All animals were born at the Washington National Primate Research Center, and were hand-reared in the Visual Neuroscience Laboratory at New York University. Their visual environment was a typical laboratory, which was enriched with a wide variety of appropriate visual and tactile stimuli. The animals were also given daily opportunities for interaction with other monkeys and humans. Ages of the animals over the course of the study ranged from 2 months to 3 years. Some animals were tested longitudinally whereas others were tested only once. All animal care conformed to guidelines approved by the New York University IACUC and the NIH Guide for Care and Use of Laboratory Animals.

Stimuli

The stimulus was a ring of co-circular Gabor patches presented in a field of randomly arrayed and randomly oriented Gabor patches. Stimuli were presented on a Nanao T660i monitor that had a mean luminance of 56 cd/m². The monitor subtended 28 deg at the usual viewing distance of 100 cm. Stimulus presentation was controlled by a PC via an ATVista graphics board (Truevision). The 792 \times 580 pixel stimulus field subtended 22×16.8 deg at 100 cm. The standard Gabor patches were made by multiplying a 3 cycles/deg sinusoid by a Gaussian with a 0.1-deg standard deviation. The contour (ring of Gabor patches) comprised 14 patches with 1.6 deg center-to-center spacing; the ring diameter was 7 deg. The noise (background Gabors) varied in density from 0.39 patches/deg² to 2.51 patches/deg². The lower bound on noise density was matched to the spacing of the patches in the ring to avoid the introduction of a density cue. Background noise density lower than that in the ring could allow the contour location to be discerned purely by detection of a zone of higher density rather than by integration of contour elements. The upper bound was constrained by the method of stimulus generation (see below). Stimulus contrast was 98%.

The placement of contour and noise elements was based on an underlying grid. Contour elements were placed first, with the constraints that only one element could occupy a grid square and that approximately constant spacing between elements was maintained. A small amount of positional jitter (25%) was allowed each contour element within its grid square so that the elements were not necessarily perfectly co-circular. Note that perfect alignment among the contour elements could create a texture nonuniformity with respect to the background, which could then be used as a cue to contour location. Noise elements were then placed randomly, with the number of noise elements per trial specified by the requested noise density. The constraints for noise-element placement were that only one element could occupy a grid square, no two noise elements could overlap, and noise elements could not overlap contour elements. The scale of the underlying grid varied with the requested noise density. At very high densities, the noise array could theoretically become regular enough to allow detection of the position of the contour by locating an irregularity in the array. Therefore we constrained the highest density used to be below this point.

To further ensure that no density cue was available in our displays, we tested two adult animals using Gaussian blobs instead of Gabor patches. Since relative orientation of the patches is the basis for linking the elements of the contour, performance should be at chance when no orientation information is present. We set the spatial frequency of the underlying sinusoid to zero to eliminate the orientation information from the patches. This manipulation results in circular rather than oriented elements, but the display is otherwise unchanged. When the density of the noise matched the spacing in the ring, performance fell to chance from near perfection for both animals with the blob stimuli, thus confirming the absence of a density cue. When noise density was set lower or higher than the delimited usable range, they could perform the task based on density (low end) or display irregularity (high end).

Behavioral methods

The subject was freely roaming in a specially designed testing cage. She initiated trials by placing her face in a mask mounted on one wall of the cage. Viewing was binocular. On each trial, the contour was presented on either the left or right side of the display monitor. The precise presentation location varied so that there was uncertainty as to where on the right or left side of the screen the contour might appear. We trained the monkeys to perform a spatial two-alternative forced-choice task using operant conditioning techniques. On each trial, they indicated on which side of the display the contour had appeared. Young monkeys (under 12 weeks) indicated their choice with an eye movement (Kiorpes & Kiper, 1996), while older monkeys (older than 12 weeks) pulled one of a pair of grab bars located on the front of the cage. Initially each stimulus was displayed for as long as the animal wished to inspect it before responding, however, some animals responded too quickly to perform optimally and others adopted a lengthy search strategy. To obtain consistent performance across subjects and ages, and to keep the task in the domain of a detection task rather than a visual search task, each stimulus was presented for only 1 s, after which time the monkeys were given 3 s to respond. Correct responses were rewarded with an age appropriate liquid (usually milk or juice); errors were signaled by a tone. Further details of our training and testing procedures can be found in earlier reports (Kiorpes et al., 1993; Kiorpes & Movshon, 1998).

To quantify contour integration performance, we measured the ability to detect the contour in increasingly dense background noise. Our measure is therefore analogous to a signal/noise analysis. Viewing distance was 50 cm for young monkeys (see above) and 100 cm for all others. Our performance measure, noise tolerance, was the background noise density at which performance fell to 75% correct. We used the method of constant stimuli to establish noise tolerance. Each tolerance estimate was based on 250–750 trials; we collected 75–150 trials at each of 3–5 noise densities chosen to span the performance range from 50% to 100% correct. 80% correct performance was required on the easiest conditions for the data to be accepted for analysis. Noise-tolerance estimates and standard errors were calculated using Probit analysis (Finney, 1971) of the log-transformed data sets.

We initially measured noise tolerance with co-circular contour elements. That is, the patches were approximately aligned along the virtual contour linking the ring of Gabors. To assess the importance of relative alignment of the contour elements, we also measured tolerance for orientation jitter of the patches in the contour. Orientation jitter could range from 0 deg to 60 deg. For a given jitter range, for example, 40 deg, the individual elements could vary in orientation with respect to alignment up to ± 20 deg in 5-deg increments. The orientation of each contour element was assigned independently within the specified jitter range. Thus, the orientation of any particular element, for this example, could be 0, 5, 10, 15, or 20 deg from alignment with respect to the contour. Data collection was counterbalanced across level of orientation jitter. Sample stimuli are shown in Fig. 1.

To characterize the effect of orientation jitter on contour integration, we fit simple Gaussian functions to the data. To fit the Gaussian, we used the data obtained starting from 0 to the maximum jitter level reached and reflected them around 0 to represent both the positive and negative limbs of the Gaussian. We extracted a bandwidth measure of orientation half-width at half-height from the fit as a measure of performance decline with orientation jitter.

To compare the development of contour integration with basic spatial resolution, we measured either grating acuity or full contrast sensitivity functions. For longitudinally tested subjects, we measured spatial resolution immediately before or at the conclusion of contour integration testing. Acuity and contrast sensitivity were measured using our conventional methods (Kiorpes, 1992; Kiorpes et al., 1993). Square-wave or sinusoidal gratings were generated under computer control with the same video display system as was used for contour integration. Grating patches were vignetted by a two-dimensional spatial Gaussian ($\sigma = 0.75$ deg, except for very low spatial frequencies for which σ was increased to keep at least three grating cycles visible). Spatial frequencies ranged from 0.3 cycle/deg to 16 cycles/deg; viewing distance ranged from 0.3 m to 2 m. The monkey's task was to detect the presence of the grating patch on either the right or left side of an otherwise homogenous gray field that matched the grating in space-average luminance. Threshold values and standard errors of estimate were obtained by Probit analysis of the log-transformed data sets (Finney, 1971) using a maximum likelihood technique. Our standard function was fit to the data and extrapolated to a contrast of 1 to estimate acuity (Kiorpes et al., 1993; Kiorpes & Kiper, 1996; Kozma & Kiorpes, 2003).

Results

The most surprising finding of this study was that monkeys younger than 4-5 months could not perform the contour integration task at any reasonable noise level. We tested three infants between the ages of 10 and 14 weeks. They could detect and indicate the location of the contour (ring of Gabors) when presented alone (no noise patches) without difficulty, but when high contrast noise was added to the display performance dropped below our criterion performance level of 80% correct. We tried a variety of manipulations of the display parameters to improve the infants' performance. First, we reduced the uncertainty in the task by removing all positional jitter from the contour. Thus, the contour appeared in a predictable location on the right or left side of the screen and local positional jitter of the elements comprising the contour was removed. We also reduced the spatial frequency of the Gabor patches and increased their size. None of these manipulations improved the infants' performance. Interestingly, they could accurately detect the contour if we added a contrast cue, so that the contour elements were higher in contrast than the noise elements. When the contrast of the noise rose above 0.5-0.75, with the contrast of the elements in the ring set at 1.0, performance fell to chance. So the animals were able to detect a contrast difference between the contour and the background but could not extract the contour from contrast-matched noise. In the end, with contour and noise matched in contrast and noise density set at the lower limit (see Methods), none of the monkeys tested could perform the task to criterion (80% correct) at ages younger than about 5 months.

Developmental data for two monkeys are shown in Fig. 2. Noise tolerance is plotted as a function of orientation jitter for all ages tested. Noise tolerance is the density of background elements at which the observer's performance falls to 75% correct (see Methods). This measure effectively represents the efficiency with which observers integrate contour information in the presence of noise. We do not use the term efficiency to represent performance with respect to a theoretical standard, since we have done no ideal observer calculation for contour integration performance (cf. Pelli, 1990). However, it is an appropriate term to describe performance of an observer in the presence of visual noise. Fig. 2A plots data from one monkey, OJ, who was among the youngest animals to master the task. The earliest data set was collected at 19 weeks; at 17 weeks she had been unable to perform the task at the criterion level of 80% correct with the lowest noise density. By 19 weeks, she could detect the contour but only when all positional jitter was removed (i.e. the elements were perfectly co-circular and the contour appeared in a consistent location on either the left or right



Jitter = 0 °

Jitter = +/- 30 °



Jitter = +/- 60 °

Fig. 1. Illustrations of the stimuli used for contour integration. We show sample contours with no orientation jitter (collinear condition), up to 30 deg of orientation jitter, and up to 60 deg of orientation jitter. In all panels the noise density is the same. The contour can be found in the lower half of each image, slightly to the right of center.

side of the screen). By 25 weeks, she was able to detect the contour with the typical positional jitter, over a small range of orientation jitter levels. Her noise tolerance was in the range of 0.8-0.9 patches/deg² at low orientation jitter and declined gradually up to 20 deg of jitter. At 50 weeks, her noise tolerance had increased over a wide range of jitter values; she was able to integrate the patches in the contour over 40 deg of orientation jitter. She apparently reached a performance asymptote by that age, which was below maximum density. When re-tested at 2 years, she had not improved further.

Data from a second monkey, RD, are shown in Fig. 2B. At 21 weeks, he was able to detect the contour at the lowest noise densities with the standard stimulus configuration (positional jitter present) and with a small amount of orientation jitter (5 deg). With maturation, he showed increased efficiency and tolerance for orientation jitter. His performance improved steadily up to 69 weeks. At that age, he was able to detect the contour in the maximum noise densities available with small amounts of orien-

tation jitter. Noise tolerance declined steadily with increasing orientation jitter, but he was still able to detect the contour with up to 60 deg of orientation jitter. When he was tested again one year later, his performance was slightly improved. For both monkeys, the noise tolerance versus jitter functions appear to be consistent in shape across age and represent simple vertically shifted replicas with increasing age.

Two aspects of the data are of interest: the change in efficiency (noise tolerance) with age, and the importance of co-circularity of the contour elements. With development the animals became more adept at integrating the elements of the contour, even in the presence of substantial orientation jitter. To capture the effects of noise and orientation jitter, in Fig. 3 we plot noise tolerance (A) and orientation sensitivity (B) as a function of age. Developmental data from individual animals are connected points; data from animals tested only once are shown as plusses. The arrow pointing to the abscissa (in Fig. 3A) represents the age before which all animals tested on the task failed to reach criterion performance.



Fig. 2. Contour integration performance as a function of orientation jitter for two monkeys tested longitudinally. Noise tolerance is the noise density (patches/deg²) at which performance fell to 75% correct; orientation jitter is the range of jitter in degrees of the elements in the contour. The arrows along the ordinate delimit the range of noise density used. (A) Data from monkey OJ at ages ranging from 19 weeks to 113 weeks. (B) Data from monkey RD at ages ranging from 21 weeks to 126 weeks.

Noise tolerance, within the limits of our task, increased steadily with age from about 5 months to approximately 18 months with some individual variation (Fig. 3A). Since some animals mastered the task at the maximum noise densities available, our data do not necessarily establish the age at which maturation is complete. However, given the various manipulations we used in attempt to find conditions under which the youngest animals could succeed, we are reasonably confident about the onset age.

To represent the effect of orientation jitter, we fit Gaussian functions (see Methods) to the data and extracted the half-width at half-height, which we plot in Fig. 3B. Bandwidths were calculated only for data sets with three or more points. There is no apparent trend toward decreasing or increasing bandwidth with age. This analysis supports our impression that the measured contour-integration functions (noise tolerance as a function of orientation jitter) are consistent in form across age and simply shift upwards to higher noise tolerance as integration efficiency improves.

Our results show that contour integration only becomes evident at about 5 months of age. However, more basic visual functions can be measured at birth or shortly thereafter. The standard benchmark for visual development, grating acuity, improves steadily



Fig. 3. Development of contour integration and orientation sensitivity. (A) Noise tolerance for the collinear contour element condition (no orientation jitter) as a function of age in weeks for individual monkeys tested longitudinally (connected points) and those tested cross sectionally. Arrows along the ordinate delimit the range of noise density used. The arrow pointing to the abscissa represents the fact that all younger animals tested failed to perform above chance. (B) Orientation sensitivity, as represented by orientation half-width (see text), as a function of age in weeks. The same symbol legend applies to panels A and B.

from birth and reaches asymptotic levels at about 24 weeks in monkeys (Boothe et al., 1988; Kiorpes, 1992). Therefore, acuity approaches adult levels in monkeys at about the same age that contour integration initially becomes evident. The relationship between acuity development and contour integration is illustrated in Fig. 4. Grating acuity and noise tolerance are plotted against the same age axis; grating acuity data refer to the left ordinate and contour integration data to the right ordinate. The data are normalized to adult performance levels in each case. Also, the ordinates are scaled so that the developmental ranges of the two data sets span the same ordinal distance. The acuity data include measures from the monkeys in the current study as well as data from infants raised for earlier studies (e.g. Kiorpes, 1992; Kiorpes & Kiper, 1996). Longitudinal data for the two monkeys whose data are shown in Fig. 2 are highlighted by the colored symbols. It is clear that acuity development is nearly complete in monkeys at the age when contour integration is just beginning to develop. Contour integration continues to develop in some animals up to 18 months. However, this should be taken as a conservative estimate of adult performance since, as mentioned above, our task is limited by the upper bound on noise density.



Fig. 4. Grating acuity and contour integration as a function of age in weeks. Grating acuity data are referenced to the left ordinate and contour-integration data to the right ordinate. The data are plotted so that each data set is normalized to normal adult values (acuity) or maximum performance (contour integration). The left and right axes are scaled so that the range of the data from the youngest to the oldest ages is comparable—no actual scale equivalence is implied. The colored symbols show developmental data for the two subjects whose data are shown in Fig. 2: OJ, red symbols; RD, blue symbols.

Discussion

We studied the development of contour integration compared to the development of basic spatial vision in macaque monkeys. Our data clearly show a later, distinct pattern of development for this global perceptual function compared to acuity. It is likely then that contour integration is not dependent on acuity development *per se* or on the mechanisms that limit maturation of spatial resolution.

We were concerned that the relatively late onset of perceptual integration skills may have been dictated by our choice of stimulus parameters and configuration. We chose the spatial characteristics of the Gabor patches to be similar to those of Kovács (2000) and to be well within the resolution range of the youngest infants in the study. We established that the young infants (10-14 weeks) could accurately indicate the location of the contour in the absence of noise and in low contrast noise. Our element separation was 1.6 deg, approximately 5λ (λ = wavelengths, the measure of spacing used commonly in other studies), which is within the range previously identified as yielding consistent performance on this task in children (Kovács et al., 1999). Kovács et al. (1999) found a decline in performance with larger element spacing but no improvement with smaller spacing. Similarly Beaudot and Mullen (2003) found relatively consistent performance in adults (better than 90% correct) on their path detection task across the element spacing range of $2-5\lambda$, although some subjects' performance declined at 5λ . It is worth noting, however, that their contours contained only ten elements, whereas ours contained 14. Pilot studies with our stimuli showed that 12-14 elements are required to produce consistently high noise tolerance.

We tried various additional manipulations of the stimulus configuration in attempt to improve infant performance. Two potential configural limitations are positional jitter and the range of noise density. We anticipated that eliminating all positional uncertainty

(local element jitter and contour positional uncertainty, which was built into the task to control for the possibility that the animals might learn to look for some specific aspect of the display) would allow them to succeed at younger ages. However, this manipulation only afforded slightly earlier acquisition of the task (OJ, 19 weeks, Fig. 2A). This suggests that the infant monkey's performance was not limited by high intrinsic positional jitter: the range of positional jitter in the standard configuration (up to 12 min) exceeds the measured equivalent intrinsic jitter in young monkeys (0.86 min on average; Kiorpes & Movshon, 1995). The lower bound on noise density was set at the average spacing among the elements in the contour to avoid the introduction of a density cue. While we did not explicitly measure the infants ability to use such a cue, successful performance under such conditions would be uninterpretable. One could not conclude that the infants were actually integrating the contour as opposed to noticing an inhomogeniety or density variation in the display. Given our efforts to improve performance in the young infants, we are convinced that stimulus limitations do not account for the late onset of contour integration we show.

Our results echo data from children showing relatively late development of perceptual organization skills (Sireteanu & Rieth, 1992; Kovács et al., 1999; Kovács, 2000). The monkeys were first able to perform contour integration reliably at 5-6 months, near the age that acuity approaches asymptotic levels. Contour integration is first measurable in children at around 36 months (range 3-5 years; Pennefather et al., 1999; Kovács et al., 1999), which is similarly near the age that acuity approaches asymptotic levels (e.g. Mayer & Dobson, 1982; Levi & Carkeet, 1993; Ellemberg et al., 1999). Kovács' studies in children suggest that contour integration development continues into the teenage years. Similarly, children show continued improvement in texture segmentation beyond age 8 years (Sireteanu & Rieth, 1992). We cannot easily place an upper bound on the monkey developmental time course since our animals' best performance was limited by the highest density that we were able to produce with our display. However, it is likely to extend over 18 months or more. Taken together, these data support the concept of an extended developmental time course for global perceptual abilities in primates.

Since our task is a signal-to-noise discrimination, it is worth considering the possibility that intrinsic noise limits performance on this task. Although we have not measured the performance of a monkey ideal observer on this task, we have real and ideal measurements for contrast discrimination in noise (Kiorpes & Movshon, 1998; Kiorpes et al., 2000; Kiorpes et al., 2003). In the behavioral study, we measured the ability of infants to detect sinusoidal grating patterns in varying levels of spatiotemporal broadband noise. We derived the quantities equivalent intrinsic noise contrast (N_{eqC}) and high noise signal/noise ratio (R_{sn}) as a function of age and spatial frequency. For frequencies in the range of the Gabor patches used for the present study, both N_{eac} and R_{sn} fall with contrast threshold during development (Kiorpes & Movshon, 1998; see also, Brown, 1994). While N_{eqC} reaches adult levels at or before the time of maturation of contrast threshold, R_{sn} continues to improve thereafter. Barlow (1977) and Pelli (1990) attribute the limitation associated with R_{sn} to central visual system factors. Central efficiency, computed according to Pelli and Farell (1999), improves from about 0.77% at 4 weeks to about 7% at 1 year (Kiorpes et al., 2003). It is plausible then that contourintegration performance depends on the relative efficiency of the central visual pathways, so that the ability to extract the contour from noise awaits developmental improvement in central signal/ noise processing. We consider below what mechanisms might provide a substrate for this late maturation.

It is widely assumed that contour integration is a cortically limited task (e.g. Field et al., 1993; Kovács, 1996). Physiological measurements of neuronal response properties in primary visual cortex of neonatal macaques show that they are surprisingly adultlike. Most receptive-field properties of V1 neurons are either already mature in 1-week-old animals (Movshon et al., 1999; Kiorpes & Movshon, 2003) or mature to adult levels by about 4 weeks (Chino et al., 1997; Hatta et al., 1998). Orientation selectivity (Movshon et al., 1999) and organization (Blasdel et al., 1995) are mature in newborns eliminating immature orientation processing as a potential mechanism. Classical receptive-field size and spatial-frequency selectivity are substantially more mature than spatial resolution in newborns and mature-to-adult levels by 16 weeks (Kiorpes & Movshon, 2003). Nonclassical surround influences are present in newborns and are comparable in strength to those in adults, however, spatial organization of the surround is different in infants (Movshon et al., 2000). These studies show that neurons in primary visual cortex, which are considered to be the primary spatial filters for the early visual pathways, are far more mature than behavioral measures spatial vision in infant monkeys (Kiorpes & Movshon, 2003). The development of V1 neurons cannot account for the development of acuity and therefore is unlikely to represent a limitation on contour integration.

Many authors have proposed that contour integration in adults depends on "long-range" horizontal connections in primary visual cortex (e.g. Field et al., 1993; Gilbert et al., 1996; Kovács, 1996; Polat et al., 1997; Stettler et al., 2002). Sireteanu and Reith (1992) and Kovács (2000) have argued that the late development of perceptual organization as measured by texture segmentation and contour integration occurs as a result of relatively late, postnatal development of such intrinsic intracortical connections (see also, Kovács et al., 1999). However, while the superficial and deep layer horizontal connections clearly develop postnatally in human infants, they mature in overall organization sometime between 4 and 15 months, and appear to be adult-like by age 2 years (Burkhalter et al., 1993). This is far earlier than the developmental profile for contour integration. A parallel relationship is found in the monkey. Coogan and Van Essen (1996) and Callaway (1998) have shown that the basic organization of local cortical circuitry is present prenatally. The intrinsic horizontal connectional system in macaque appears to be adult-like at birth or shortly thereafter (Coogan & Van Essen, 1996; Levitt & Lund, 1996; Lund & Levitt, 1996). While the published data are somewhat limited, they indicate that the long-range intracortical connectional system is structurally mature well before contour integration begins to develop.

Recent anatomical and physiological studies demonstrate that the extent of the long-range horizontal connections in primate V1 are matched to the extent of the *excitatory* summation area of the receptive field, but do not account for the full extent of the modulatory surround (Sceniak et al., 2001; Angelucci et al., 2002; Cavanaugh et al., 2002; Levitt & Lund, 2002). These studies further suggest that the extent of the modulatory, *inhibitory* surround of V1 neurons can be ascribed to feedback projections from extrastriate areas with large receptive fields. The measured sizes of the modulatory surrounds are in fact well matched to the feedback projection fields of V3 neurons (Angelucci et al., 2002). Reciprocal connections between V1 and V2 appear to develop concurrently with or soon after the intrinsic horizontal projections in cat (Callaway & Katz, 1990), monkey (Coogan & Van Essen, 1996), and human (Burkhalter, 1993). Beyond V2, dorsal and ventral stream feedback projections in macaques are present at birth but undergo an extended period of remodeling compared to feedforward projections; this period extends up to 2–3 months postnatal (Barone et al., 1995; Batardière et al., 2002). Therefore, although these reciprocal connections are present relatively early in devel-

opment, the postnatal remodeling may contribute to spatial reorganization of the modulatory surround of V1 neurons. Such reorganization (noted above) was found to take place between 4 and 16 weeks (Movshon et al., 2000). It is possible then that contour integration capability develops only after the inhibitory surround organization has fully matured.

In further consideration of the potential of V1 as the important site for a contour integration task such as ours, it is worth examining the spatial scale of V1 receptive fields. Recall that intrinsic horizontal connections define the limit of the excitatory center of V1 receptive fields (see above). The average size of V1 area summation fields (which correlate with the excitatory center regions) ranges from about 0.8 deg foveally to 2.1 deg in the periphery (Sceniak et al., 2001; Cavanaugh et al., 2002), although neurons with substantially larger summation areas are reported (see Levitt & Lund, 2002). These are larger than the original estimates of receptive-field size, which were based on the minimum response field (e.g. Hubel & Wiesel, 1968), and were in the range 0.25-0.5 deg for central V1. The stimuli used in our experiments consisted of contour elements spaced 1.6 deg center-tocenter, which is in the same range as was used by Kovács and others. While current estimates of V1 receptive-field size are substantially larger than previous estimates, they are not so large as to allow integration of multiple elements along our contour. An individual excitatory receptive-field center may be large enough to include two adjacent elements but would not include more than two. Moreover, elements of like orientation falling in the zone of the inhibitory surround will reduce the response to elements within the center (Knierim & Van Essen, 1992; Kapadia et al., 1995; Sceniak et al., 2001; Cavanaugh et al., 2002; Levitt & Lund, 2002) rather than enhance it. Therefore, a ring or a snake of similarly oriented Gabors would in fact be expected to disrupt performance as the contour length is increased, which is not the case in psychophysical studies (Field et al., 1993; Levi et al., 1997; Pettet et al., 1998; Geisler et al., 2001). On the contrary, performance improves as the number of elements comprising the contour is increased, and in our task a minimum of six patches was required for successful contour detection. Thus, it seems unlikely that V1-including its system of intrinsic horizontal connectionsdirectly supports contour integration performance, which implies a substrate beyond V1 (see also, Hess & Field, 1999; Geisler et al., 2001; Herzog & Fahle, 2002).

The foregoing analysis suggests that all of the important connectivity of V1 neurons, intracortical and possibly intercortical, is established before birth or matures coincidently with the maturation of grating acuity, and before the development of contour integration. Thus it makes sense to look beyond V1. It is well known that neurons in extrastriate areas have larger receptive fields than neurons in V1. Neurons in V2 and V3, for example, have receptive fields (minimum response fields) that are 2–6 times larger than those in V1 (Gattass et al., 1981; Felleman & Van Essen, 1987) and are therefore better suited to integration of information over distances such as those required for contour integration. Furthermore, there is evidence that visual responses in some extrastriate visual areas develop later than in striate cortex (Bachevalier et al., 1991; Rodman et al., 1993; Rodman, 1994; Distler et al., 1996). Recent fMRI studies of adult primates show enhanced responses in several extrastriate areas to shape and contour-linking stimuli as well as activation in V1 (Altmann et al., 2003; Kourtzi et al., 2003). These authors suggest that the responses in early visual areas may arise from feedback from higher areas, with the final coherent percept forming in areas such as lateral occipital complex (LOC). This interpretation is consistent with current neurophysiology in behaving primates showing a late enhancement of neuronal responses in V1 to complete figures or contours which follows the initial response to individual stimulus elements (Zipser et al., 1996; Lamme et al., 1999; Lamme & Roelfsema, 2000; but see Bauer & Heinze, 2002, for a different interpretation).

In summary, we find late development of global perceptual skills in the macaque monkey, as exemplified by contour integration. This late maturation parallels what has been reported in humans. Our data are consistent with the notion that infant visual sensitivity is hampered by high levels of noise in the central visual pathways. The source of this noise is unknown. However, given the current state of knowledge of V1 development, there are no obvious significant immaturities to explain late development of perceptual organization at that level. Primary development of neuronal mechanisms beyond V1, which serve either independently or in the form of remodeling of feedback projections from higher cortical areas to V1, remain intriguing possibilities.

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