Development of orientation tuning in simple cells of primary visual cortex

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Moore BD 4th, Freeman RD. Development of orientation tuning in simple cells of primary visual cortex. J Neurophysiol 107: 2506–2516, 2012.—Orientation selectivity and its development are basic features of visual cortex. The original model of orientation selectivity proposes that elongated simple cell receptive fields are constructed from convergent input of an array of lateral geniculate nucleus neurons. However, orientation selectivity of simple cells in the visual cortex is generally greater than the linear contributions based on projections from spatial receptive field profiles. This implies that additional selectivity may arise from intracortical mechanisms. The hierarchical processing idea implies mainly linear connections, whereas cortical contributions are generally considered to be nonlinear. We have explored development of orientation selectivity in visual cortex with a focus on linear and nonlinear factors in a population of anesthetized 4-wk postnatal kittens and adult cats. Linear contributions are estimated from receptive field maps by which orientation tuning curves are generated and bandwidth is quantified. Nonlinear components are estimated as the magnitude of the power function relationship between responses measured from drifting sinusoidal gratings and those predicted from the spatial receptive field. Measured bandwidths for kittens are slightly larger than those in adults, whereas predicted bandwidths are substantially broader. These results suggest that relatively strong nonlinearities in early postnatal stages are substantially involved in the development of orientation tuning in visual cortex.

orientation selectivity; vision; nonlinearity

THE TRANSFORMATION OF RECEPTIVE FIELDS (RFs) from center-surround organization in the early visual pathway to that of elongated edges in striate cortex is accompanied by the property of orientation selectivity of cortical neurons. Although orientation tuning is present at early postnatal stages, it narrows developmentally to a final adult level of selectivity (Bonds 1979; Freeman and Ohzawa 1992). Regarding the derivation of simple cell orientation selectivity, there is evidence supporting both feedforward and intracortical processing (see Ferster and Miller 2000 for a review). The classical model of orientation selectivity involves a hierarchical processing of information occurring from convergent arrays of feedforward lateral geniculate nucleus (LGN) input onto simple cells in area 17 of the visual cortex (Hubel and Wiesel 1962). Tests of this model have included direct recordings from LGN afferents (Chapman et al. 1991) and simultaneous recordings from pairs of monosynaptically connected LGN and simple cells (Reid and Alonso 1995; Tanaka 1983). In other tests, intracellular recordings of simple cells have been made while primary visual cortex was presumably inactivated. Reported findings indicate that specificity of orientation tuning can be accounted for entirely by thalamic input (Chung and Ferster 1998; Ferster et al. 1996). In addition, synaptic input to simple cells is reported to be approximately linear, which is consistent with the original hierarchical model of orientation specificity (Jagadeesh et al. 1997).

Alternative evidence suggests that linear summation of feedforward input cannot account for all the orientation-selective properties of cortical cells. Intracellular recordings of simple cells indicate that the spiking output of these neurons is more narrowly tuned than the synaptic input (Finn et al. 2007; Volgushev et al. 1996, 2000). The assumption is that if thalamic input is linear, nonlinear effects involved in orientation tuning processes must be cortical (Jagadeesh et al. 1997). The influence of cortical processes on simple cell orientation selectivity has been considered in different models of central visual pathway function (Chance et al. 1999; Douglas et al. 1995; Somers et al. 1995; Vidyasagar et al. 1996). The general assumption is that cortical mechanisms, and in particular the nonlinearity introduced by a spike threshold, play a clear role in the refinement of simple cell orientation tuning (Carandini and Ferster 2000; Finn et al. 2007; Volgushev et al. 2000).

Linear and nonlinear contributions to orientation selectivity of simple cells have been estimated previously by comparing measured tuning with predictions made from linear summation across spatial RF profiles. Results of studies using extracellular spike rate measurements indicate that most simple cells exhibit sharper measured orientation tuning compared with what is predicted by linear spatial processes (Gardner et al. 1999; Li et al. 2003; Usrey et al. 2003). However, a similar procedure conducted intracellularly found a strong agreement between orientation tuning predicted from spatial RFs and that measured using gratings (Lampl et al. 2001). The discrepancy between the intracellular and extracellular studies noted above suggests that the spike threshold exerts a larger effect on responses to oriented gratings than on RFs calculated on the basis of linear spatial summation.

We consider here the development of orientation selectivity in the central visual pathway with respect to linear and nonlinear processes in kittens and in adult cats. To do this, we have computed predicted orientation tuning by visual activation from linear summation across simple cell spatial RFs. We have compared the predicted values with measured orientation tuning results obtained by use of conventional drifting sine wave grating stimuli. Our findings indicate that predictions of orientation tuning bandwidths based on linear spatial summation are broader in young kittens, compared with those found in adults, whereas measured bandwidths are similar in the two groups. These results show that nonlinear mechanisms during development of orientation tuning are relatively strong compared with those in adults. This finding indicates that cortical mech-
Anisms play a substantial role in the development of orientation tuning and presumably other response properties of first-stage cells in the visual cortex.

METHODS

Physiological procedures. This work has been approved by the University of California animal care and use committee as protocol R075. Previous descriptions of our general physiological procedures have been published (Anzai et al. 1999a, 1999b; DeAngelis et al. 1993a, 1993b; Li and Freeman 2010). In brief, extracellular recordings are made from isolated simple cells in the striate cortex of anesthetized and paralyzed mature cats or 4-wk postnatal kittens using tungsten-in-glass microelectrodes (Levick 1972). For mature animals, penetrations are made along the medial bank of the postlateral gyrus through a craniotomy centered at 4 mm posterior and 2 mm lateral from zero Horsley–Clarke stereotaxic position (Horsley and Clarke 1908). For kittens, electrode penetrations are made through a craniotomy ∼2–3 mm anterior and 1–2 mm lateral to the lambda suture, a prominent feature at the dorsal edge of occipital lobe. After single units are isolated, preferred values are determined quantitatively for orientation, spatial frequency, position, and RF characterics by use of drifting sinusoidal gratings. RFs were between 0° and 15° eccentric. For this study, we used simple cells identified on the classic basis of internal structure of the spatial RF (Hubel and Wiesel 1962) and the degree of first harmonic modulation in responses to drifting sinusoidal gratings (Skottun et al. 1991). Orientation tuning curves are established quantitatively by use of the first harmonic response to gratings at optimal spatial frequencies and a drift rate of 2 Hz. To do this, gratings are presented monocularly at seven or more orientations in 10° to 15° increments on both sides of the preferred orientation. Each stimulus is presented for 4 s, followed by an interstimulus interval of 2–4 s, and the order of presentation is randomized. High grating contrasts are used to elicit strong responses, and blank stimuli are employed to estimate spontaneous activity for each cell.

We also obtained spatiotemporal RF maps by use of dynamic sparse white noise stimuli and a reverse correlation technique as described elsewhere (de Boer and Kuyper 1968; Eggremont et al. 1983; Jones and Palmer 1987a, 1987b; Sutter 1975). Details of the technique we have used have been described previously (DeAngelis et al. 1993a). Briefly, a rectangular stimulus is divided into a 20 × 20 grid oriented along each neuron’s preferred orientation and presented within the classical RF. Bar stimuli within the patch have high (32 cd/m2) or low luminance (2 cd/m2) and are distributed sequentially at random grid locations for 40-ms durations. Mean background luminance is 20 cd/m2. Cross-correlation of the resulting spike train with the stimulus pattern yields a linear approximation of the space-time RF profile.

Data analysis. Orientation tuning width (half-width at half-height), preferred orientation, and response amplitude are quantified by Gaussian fits to peaks of orientation tuning curves using a constrained nonlinear maximum likelihood optimization procedure (Matlab mfile). The Gaussian function is given by

\[ r(\theta) = Ae^{-(\theta - \theta_{\text{opt}})^2/2\sigma_\theta^2} + A_{\text{off}} \]

where \( r(\theta) \) is the amplitude at orientation \( \theta \); parameters \( A \) and \( A_{\text{off}} \) are the peak response amplitude and amplitude offset, respectively; \( \theta_{\text{opt}} \) denotes the peak of the Gaussian (the preferred orientation); and \( \sigma_\theta \) is the standard deviation. Half-width of the orientation tuning curves is defined as one-half the width of the Gaussian at one-half the maximum height above \( A_{\text{off}} \) and is equal to 1.17\( \sigma_\theta \). In general, these fits captured a high proportion of the variance (median adult \( r^2 = 0.9657 \); median kitten \( r^2 = 0.9433 \)).

Predicted orientation tuning curves are computed to estimate linear and nonlinear contributions to orientation selectivity, as described previously (Gardner et al. 1999). Orientation tuning is predicted by application of a discrete Fourier transform to each cell’s two-dimensional (2-D) spatial RF. Predicted responses are obtained by a sampling of points in the amplitude spectrum along a semicircle centered at the origin and having a radius corresponding to the spatial frequency of the sine wave gratings used to measure orientation responses. The amplitude of each point along this arc through the frequency amplitude spectrum is taken as the predicted response to a sine wave grating at that particular orientation. Each cell’s predicted orientation tuning curve is fit with a 1-D Gaussian to quantify the bandwidth (half-width at half-height, as above; median adult \( r^2 = 0.9614 \); median kitten \( r^2 = 0.9216 \)).

Each cell’s output nonlinearity is quantified by first sorting the measured responses from lowest to highest. These responses are then compared with the amplitude of the frequency spectrum at the corresponding orientations. The data are then plotted on log-log coordinates, and a straight line is fitted to the relationship (median adult \( r^2 = 0.9888 \); median kitten \( r^2 = 0.9730 \)). The slope of this line is taken as an estimate of the power function exponent for each cell (Anzai et al. 1999a; Duong and Freeman 2008). A second method of calculating exponents, as used in previous studies (Gardner et al. 1999; Li et al. 2003), produced similar results to those presented here.

RF length is estimated by integration along a 1° slice through the 2-D RF envelope at 37% of the maximum amplitude. The slice is parallel to the preferred orientation and passes through the point of maximum RF energy. For RFs with subunits of unequal lengths, the length of the longest subunit is used. RF width is estimated by integration across a 1° slice orthogonal to the preferred orientation and passing through the point of maximum RF energy. Aspect ratio is defined as the ratio of RF length to RF width. Where stated, population means are accompanied by standard errors.

RESULTS

We used an analytical approach that assumes a fundamental sequence of processing for orientation selectivity as illustrated in Fig. 1A. In this diagram, a sine wave grating stimulus is filtered by center-surround retinal and LGN neurons. The output from an elongated array of LGN neurons then projects to a simple cell, which also receives linear cortical inputs, resulting in a linear simple cell RF filter that is elongated along one axis and contains multiple subregions. Before the output of the simple cell is transformed into action potential response, it is subjected to a static expansive nonlinearity (Albrecht and Geisler 1991; Anzai et al. 1999a; DeAngelis et al. 1993a; see Ferster and Miller 2000 for a review).

The effects of expansive output nonlinearities on orientation tuning are explored in Fig. 1, B and C. Figure 1B shows a schematic orientation tuning curve that has undergone transformation by various output nonlinearities of different strengths, which are quantified as power function exponent values. The input tuning curve is shown in black. The gray curves show the same schematic tuning curve when output nonlinearities are imposed. Note that the tuning curve becomes substantially narrower at high exponent values. The effects of expansive output exponents on orientation tuning bandwidth are illustrated in Fig. 1C. The horizontal axis shows orientation tuning bandwidth before the output nonlinearity, whereas the vertical axis shows orientation tuning following the output nonlinearity. The black line depicts a linear relationship, and the family of gray traces illustrate the effects of various nonlinear exponent values. The gray traces convey the notion that expansive exponents signify substantially lower orientation tuning bandwidths.
We analyzed RF maps and orientation tuning curves from 91 simple cells in the primary visual cortex. Of these, 52 were from 11 mature cats and 39 were from 16 4-wk postnatal kittens. For these animals, protocols for other experiments were also employed. In the current study, experimentally determined spatial RF maps were used to predict orientation tuning bandwidths, which were then compared with those observed in response to drifting sinusoidal gratings. Results of this analysis for a typical simple cell from the mature group are illustrated in Fig. 2. The 2-D RF profile is illustrated in Fig. 2A. This was determined by use of a dynamic white noise stimulus to yield the detailed RF map in both space and time. The profile of this spatiotemporal RF at the correlation delay that produces the largest sum of squared response is then taken as the spatial RF that is used for subsequent analysis. Regions of visual space that are excited by bright or dark spots are enclosed by solid or dashed contour lines, respectively. Note that this example simple cell has two adjacent parallel elongated sub-regions, which is typical and has been noted in previous studies (Alonso et al. 2001; DeAngelis et al. 1993a, 1993b; Jones and Palmer 1987a; Reid et al. 1997).

A spatial RF depiction is illustrated with contour lines in Fig. 2A. From this pattern, we calculated the frequency domain transform of the spatial RF, which are symmetrical components, as illustrated in Fig. 2B. Figure 2B contains a semicircle with a radius set by the optimal spatial frequency value determined by use of drifting sinusoidal gratings. The amplitude of the frequency domain profile along the semicircle yields a predicted orientation tuning curve generated from the frequency domain analysis, as illustrated in Fig. 2C. The measured orientation tuning curve for this cell, as shown in Fig. 2D, is a typical response to a grating drifting in the neuron’s preferred direction (red) and a corresponding Gaussian fit (blue). The error bars depicted in Fig. 2D represent one standard error and are representative of the response variance encountered for other cells in our population. For this example simple cell, measured bandwidth is lower (12°) than that

Fig. 1. Schematic diagram of a basic orientation tuning sequence. A: the stimulus, in this case a drifting sine wave grating, is first filtered by retinal and lateral geniculate nucleus (LGN) cells. Convergent output from an array of LGN cells is then linearly summed with linear cortical input by the simple cell, resulting in the characteristic elongated receptive field (RF) profile. Before output from the simple cell, the signal is subjected to an expansive output nonlinearity, which has the effect of reducing responses to nonoptimal stimuli. B: schematic of orientation tuning curves following static output nonlinearities of various strengths. Orientation tuning before output nonlinearity is shown in black. Curves illustrating orientation tuning following output nonlinearities of various exponent strengths (n) are shown in gray; these show substantially lower bandwidths than the original tuning curve. C: relationship between orientation tuning bandwidth before and after expansive output nonlinearity. The black line depicts a linear relationship. Gray lines show orientation tuning at various nonlinear output exponent values; these curves illustrate that orientation tuning bandwidths following output nonlinearities are sharper and that higher exponent values impose more sharpening.

Fig. 2. Analysis used to measure linear/nonlinear contributions to simple cell orientation tuning. A: contour plot of a spatial RF profile for an example simple cell. Regions of visual space that are responsive to bright or dark spots are enclosed by solid or dashed contour lines, respectively. Note that this example simple cell has two adjacent parallel elongated sub-regions, which is typical and has been noted in previous studies (Alonso et al. 2001; DeAngelis et al. 1993a, 1993b; Jones and Palmer 1987a; Reid et al. 1997).

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predicted from spatial analysis (25°). The data illustrated in Fig. 2 are typical of the simple cells in our sample. In general, the neurons are highly tuned for grating orientation and generally have bidirectional responses, although drift in one direction is frequently dominant. Whereas the magnitude of responses to gratings drifting in different directions frequently differs, peaks for preferred and nonpreferred directions have similar bandwidths (Campbell et al. 1968). In the current study, we measured bandwidths using the direction of grating drift that generated the highest responses.

To illustrate the range of response types that we observed, representative tuning functions are shown in Fig. 3 for four cells each from mature cats and kittens. The same RF subregion format used in Fig. 2 is employed here; areas excited by bright or dark spots are enclosed, respectively, by solid or dashed contours. Typical RF patterns include two subregions. Although less common, we also observed some with three bright or dark spots are enclosed, respectively, by solid or dashed contours. Typical RF patterns include two subregions.

As noted above, each orientation tuning curve for our sample of cells was fitted with a Gaussian function. From these functions, we quantified tuning bandwidths and plotted predicted vs. measured values for adult (filled circles) and kitten neurons (open circles) in Fig. 4. Note that most data points are below the diagonal line with unity slope. Therefore, measured responses are sorted from lowest to highest magnitude of the tuning curve predicted from the linear RF. Specifically, measured responses are sorted from lowest to highest and compared with the amplitude of the predicted tuning curve at corresponding orientations (see METHODS). The magnitude of the nonlinear power function exponent is then estimated as the slope of a straight line fit to the relationship in log-log coordinates (Anzai et al. 1999a). Data for an example cell are shown in Fig. 6, A and B. For exponent values <1, nonlinearities are compressive, whereas those >1 are expansive.

Distributions of exponent values for kitten and adult cell populations are presented in Fig. 6, C and D, respectively. For the adult population represented in Fig. 6D, the mean is 4.43 ± 0.67, which is an expansive value. It indicates that the linear spatial RF is insufficient to account for the sharpness of orientation tuning and that other mechanisms are needed to refine orientation tuning to the measured values. For the neuronal group from kittens represented in Fig. 6C, the mean exponent value is almost twice that for adults, 8.18 ± 1.36. The difference is significant (P = 0.0342, Wilcoxon rank-sum test). The data in Fig. 6 demonstrate clearly that the exponents required to account for the discrepancy between predicted and measured bandwidths are substantially higher in kittens compared with adults. The implication is that nonlinearities during the critical early developmental stages of the visual system, which we assume are derived from intracortical processes, play a vital role in the refinement of orientation tuning. Although the developmental process of orientation tuning has been studied previously, we are not aware of any similar analysis or conclusion from earlier investigations.
Fig. 3. Examples of analysis for neurons from adult and kitten populations. RFs with predicted and measured orientation tuning are shown for 4 cells from each group. A–D illustrates the spatial RF configuration for adult simple cells. Areas excited by bright spots are enclosed by solid contour lines, and areas excited by dark spots are enclosed by dashed contours. Cells typically have 2 subunits, like those shown in B and D, although some possess additional subunits, like those shown in A and C. The corresponding measured orientation tuning curve for each adult cell is shown in A₁–D₁ (solid line); the orientation tuning curve predicted from the spatial RF is shown as a dashed line. The amplitude of the predicted tuning curve has been normalized to the peak response of the measured curve for illustration purposes. Four example kitten RFs are shown in E–H, along with the corresponding measured and predicted tuning curves (E₁–H₁). For all the cells depicted, there is a good agreement between the measured and predicted preferred orientation, with the exception of the cell shown in F. There is a range of discrepancy between predicted and measured tuning bandwidths. The linear spatial RF accurately predicts the measured tuning bandwidth of the adult cell shown in A and the kitten cell shown in H. For other cells, such as the adult cell shown in C and the kitten cell shown in F, however, there is a larger discrepancy between the predicted and measured tuning curves, indicating that nonlinear processing sharpens orientation tuning beyond that presented by the spatial RF.
To further analyze the relationship between orientation tuning development and neural nonlinearities, we next examined orientation bandwidth as a function of exponent values, as shown in Fig. 7. Predicted and measured bandwidths are examined, respectively, as a function of exponent values in Fig. 7, A and B. For adult simple cells (filled circles), there is a significant positive correlation between exponent value and predicted bandwidth ($r^2 = 0.1708$, $P < 0.01$). This type of correlation does not apply in the case of kitten simple cells (open circles). For kittens, $r^2 = 0.0742$ and $P = 0.0921$, indicating that exponent values do not correlate with predicted bandwidths. In the case of measured bandwidths, Fig. 7B shows a significant negative correlation for kitten simple cells ($r^2 = 0.1771$, $P < 0.01$). In other words, neurons with high exponent values have relatively narrow measured tuning bandwidths. There is a similar relationship for adult simple cells ($r^2 = 0.1826$, $P < 0.01$).

Our analysis approach, as illustrated in Fig. 2, involves predicted vs. measured orientation tuning curves. The prediction approach involves estimated bandwidths from the spatial RF vs. orientation tuning bandwidth measured with sinusoidal gratings. Filled circles correspond to bandwidths from adult animals, and open circles correspond to bandwidths from kittens. The dashed line indicates bandwidth means for all neurons in our sample (mean predicted bandwidth = 38.51° ± 1.38°; mean measured bandwidth = 21.58° ± 1.21°).
predicted curve is taken as the amplitude of the frequency domain profile along an arc with a radius determined by the neuron’s optimal spatial frequency. The bandwidth of each predicted orientation tuning curve is therefore dependent on both the profile of the frequency domain RF and the optimal spatial frequency. Previous findings show that spatial frequency selectivity of cortical neurons in the cat is relatively low in early postnatal days and develops rapidly to adult levels by 5 or 6 wk postnatal (Derrington and Fuchs 1981; Freeman and Ohzawa 1992). Our current results show that orientation tuning bandwidths predicted from kitten spatial RFs are significantly broader than those from adult animals. It is of obvious interest to determine whether optimal measured spatial frequency is correlated with predicted orientation tuning bandwidth. To examine this, we plotted optimal spatial frequency distributions of the neurons in our samples from kittens and adult cats. As shown in Fig. 8, optimal spatial frequency values are, as expected, higher for adult (0.52 ± 0.04 cycles/deg) compared with kitten simple cells (0.30 ± 0.03 cycles/deg), and the difference is significant (P < 0.01).

Optimal spatial frequencies are lower for kittens compared with adult cats, and predicted bandwidths are dependent on optimal spatial frequencies. Therefore, cells with low optimal spatial frequencies should have relatively high predicted bandwidths. To examine this, predicted tuning bandwidths are compared with optimal spatial frequencies in Fig. 8C. As the data show for both kittens and adults (open and filled circles, respectively), there is an inverse relationship between spatial frequency and predicted orientation selectivity (r² = 0.2794, P < 0.01 and r² = 0.1133, P < 0.05, for kittens and adults, respectively). Thus there is a clear correlation between development of peak spatial frequency values and predicted orientation tuning bandwidths.

An obvious parameter in the study of orientation selectivity is the inherent spatial structure of the simple cell RF. Specifically, the size, shape, spacing, and numbers of RF subunits are of clear interest. Although we did not quantify the number of simple cell subunits because of the difficulty in accurately measuring that value, we did explore several other parameters related to RF structure. We measured length, width, and aspect ratio of the simple cell RFs in our samples (see METHODS for details). Measurements of these parameters are shown in histogram form for kitten and adult neurons in Fig. 9. With regard to RF length (Fig. 9, A and B), we found similar values in adults compared with kittens (2.67° ± 0.10° vs. 2.51° ± 0.10°; P = 0.28). Three adult cells were excluded from this analysis due to difficulties in measuring RF length. Similarly, RF widths (Fig. 9, C and D) were approximately equal in our adult cat and kitten samples (1.84° ± 0.12° vs. 1.89° ± 0.12°; P = 0.81). Aspect ratios (Fig. 9, E and F), which were computed for each neuron, were slightly higher for adult compared with kitten populations (1.65 ± 0.08 vs. 1.54 ± 0.12; P = 0.4742), but this difference is not significant.

These same RF parameters of length, width, and aspect ratio were also examined with respect to predicted and measured bandwidths, as shown in Fig. 10. For predicted and measured bandwidths, there are no correlations between RF length (Fig. 10, A and B) and bandwidths for either adult or kitten populations (adult predicted r² = 0.0110, P = 0.4730; adult measured r² = 0.0040, P = 0.6658; kitten predicted r² = 0.0001, P = 0.5512; kitten measured r² = 0.0001, P = 0.9419). For width parameters (Fig. 10, C and D), there are no correlations for the kitten cell population (predicted r² = 0.0138, P = 0.4756; measured r² = 0.001, P = 0.9561). Measured orientation tuning bandwidth for adults is weakly correlated with RF length (r² = 0.0815, P = 0.0402), but predicted bandwidth is

Fig. 8. Preferred spatial frequencies for adults and kittens. Spatial frequency tuning was assessed using drifting gratings. Adult simple cells (A) have a higher mean optimal spatial frequency than kitten simple cells (B; 0.52 ± 0.04 vs. 0.30 ± 0.03 cycles/deg; P < 0.01). C: orientation tuning bandwidth predicted from the spatial RF vs. preferred spatial frequency. There is an inverse relationship between optimal spatial frequency and the predicted bandwidth for both kitten (r² = 0.2794, P < 0.01) and adult simple cells (r² = 0.1133, P < 0.05). c/d, Cycles/deg.
not ($r^2 = 0.0181, P = 0.3422$). Aspect ratio is weakly correlated with predicted bandwidths in adults but not kitten cells (Fig. 10E; $r^2 = 0.1920, P < 0.01$; and $r^2 = 0.1046, P = 0.0446$, respectively). For measured orientation tuning, there is a weak correlation with aspect ratio for adults but not for kittens (Fig. 10F; $r^2 = 0.1358, P < 0.01$; and $r^2 = 0.0152, P = 0.4551$, respectively). A similar relationship between aspect ratio and bandwidth has been reported previously for adult cortical neurons (Gardner et al. 1999). Considered together, these findings indicate that the linear RF structure plays a relatively larger role in the determination of orientation selectivity in mature visual cortex compared with young kittens.

Our main findings of predicted vs. measured tuning bandwidths, as shown in Fig. 4, show that the main contribution to orientation selectivity in cortical simple cells is via linear spatial RF structure. Presumably, nonlinear cortical mechanisms contribute to the refinement of orientation tuning. To determine whether the degree of nonlinearity is related to RF structure, we compared length, width, and aspect ratio with exponent values for each cortical simple cell.

The relationships of these parameters, as shown in Fig. 11, indicate an absence of correlations between exponent values and the RF variables of length, width, and aspect ratio for adults and kittens (length, Fig. 12A; $r^2 = 0.0006, P = 0.5912$; and $r^2 = 0.0265, P = 0.3221$; width, Fig. 12B; $r^2 = 0.0572, P = 0.0878$; and $r^2 < 0.01, P = 0.5753$; aspect ratio, Fig. 12C; $r^2 < 0.01, P = 0.7348$; and $r^2 = 0.0148, P = 0.4609$, for adults and kittens respectively). It appears, therefore, that RF structure is not specifically related to the degree of nonlinearity in either of the two cortical populations we have studied.

**DISCUSSION**

We have examined the development of orientation tuning in the primary visual cortex of the cat. Our analysis concerns cortical simple cells that are thought to receive linear feedforward input from the LGN. We assume that the spatial organization of simple cell RFs generated from spike responses can be used to make predictions about linear contributions to orientation tuning. This analysis provides a direct assessment of linear and nonlinear contributions to simple cell orientation tuning. We have carried out this analysis for cortical simple cells in adult cats and for kittens at age 4 wk postnatal. Our approach is to compare orientation tuning curves of adult and

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Fig. 9. Measurements of kitten and adult RF structure, including length, width, and aspect ratio. A: adult RF lengths (mean $= 2.67^\circ \pm 0.10^\circ$). B: kitten RF lengths (mean $= 2.51^\circ \pm 0.10^\circ$). There is no significant difference between adult and kitten RF lengths ($P = 0.28$). C: adult RF widths (mean $= 1.84^\circ \pm 0.12^\circ$). D: kitten RF widths (mean $= 1.89^\circ \pm 0.12^\circ$). There is no significant difference between adult and kitten RF widths ($P = 0.81$). E: adult RF aspect ratios (mean $= 1.65 \pm 0.08$). F: kitten RF aspect ratios (mean $= 1.54 \pm 0.12$). There is no significant difference between adult and kitten RF aspect ratios ($P = 0.4742$).

Fig. 10. Relationship between RF structure and orientation tuning bandwidths. A: relationship between RF length and predicted orientation tuning. There is no correlation for either adult or kitten simple cells ($r^2 = 0.0110, P = 0.4730$; and $r^2 = 0.0001, P = 0.5512$, respectively). B: relationship between RF length and measured orientation tuning for adults and kittens. There is no correlation for either adult or kitten simple cells ($r^2 = 0.0040, P = 0.6658$; and $r^2 = 0.0001, P = 0.9419$, respectively). C and D: relationships between RF width and predicted (C) and measured (D) orientation tuning. Neither the predicted nor measured orientation tuning bandwidths for kittens are significantly correlated ($r^2 = 0.0138, P = 0.4756$; and $r^2 = 0.001, P = 0.9561$, respectively). Measured orientation tuning bandwidth for adults is weakly correlated with RF length ($r^2 = 0.0815, P = 0.0402$), but predicted bandwidth is not ($r^2 = 0.0181, P = 0.3422$), and $r^2 = 0.0040, P = 0.6658$; and $r^2 = 0.001, P = 0.9561$, respectively).

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kitten cortical cell populations by use of drifting sine wave gratings. Bandwidths are predicted from linear spatial RF profiles. For the population of cortical simple cells that we have studied, measured bandwidths are similar in kittens and adults. However, predicted bandwidths in kittens are substantially broader.

Our estimates of nonlinear contributions to orientation tuning are determined by derivations of exponent values in each population. The exponents are derived by estimation of the difference between linear predictions of orientation tuning and measurements with sine wave gratings. Specifically, exponent values are taken as the slopes of straight line fits to the relationship between measured responses and predicted amplitudes in log-log coordinates (Anzai et al. 1999).

For each neuron, exponent values greater or less than 1.0 reflect the degree of influence exerted by nonlinear mechanisms on orientation tuning. This provides a quantitative analysis of linear and nonlinear contributions. We found expansive processes, i.e., processes serving to sharpen rather than broaden orientation tuning, for both populations of neurons. However, exponent values are significantly higher for neurons from kittens, compared with those from adults. Although tuning can be accounted for in part by changes in spatial characteristics of linear spatial RF profiles, nonlinear mechanisms, presumably within visual cortex, are especially prominent in the refinement of orientation tuning in kittens.

Orientation selectivity is a primary property of neurons in visual cortex, and it has been studied from both experimental and theoretical perspectives. In the steady-state mature case, orientation selectivity of simple cells was originally proposed to be the result of input from elongated arrays of LGN neurons with center-surround configurations (Hubel and Wiesel 1962). The assumption was that there is a simple linear summation of input from LGN cells. Subsequent intracellular recordings from simple cells have demonstrated that thalamic input is linear, in accordance with this model (Jagadeesh et al. 1997). A more powerful experimental approach was to record simultaneously from monosynaptically connected LGN and visual cortical neurons that shared common RF space. Once again, the serial processing feedforward model was consistent with obtained data (Alonso et al. 2001; Reid and Alonso 1995).

However, the serial processing hierarchical model of simple cell orientation selectivity is inconsistent with some findings. For example, linear summation of individual intracellular postsynaptic potentials can accurately account for a given cell’s optimal orientation but not its tuning bandwidth (Volgushev et al. 1996; but see Lampl et al. 2001). Some nonlinear processes have been described in the retina (Benardete and Kaplan 1999; Shapley and Victor 1978) and LGN (Duong and Freeman 2008), but intracellular recordings in simple cells indicate that LGN input is linear. The additional orientation tuning refinement that is not accounted for by a simple serial feedforward processing mechanism could be due to expansive static nonlinearities at the output stage of simple cells (Gardner et al. 1999). The expansive static nonlinearity could be the result of interactive processes between membrane potential and action potential thresholds (see Ferster and Miller 2000).

The contribution of a spike threshold mechanisms to orientation tuning has also been investigated (Carandini and Ferster 2000; Volgushev et al. 2000). Apparently, no intracellular studies have focused on orientation tuning in immature kitten visual cortex. Expansive nonlinearities have also been studied in connection with contrast adaptation. For example, contrast adaptation is very strong in young kittens (Sclar et al. 1985). This effect could be similar to that found in different types of expansive nonlinearities.

The factor most likely to account for the strong nonlinear control of orientation tuning in young animals is a spike threshold mechanism. It may be involved as follows. The greater the difference between the baseline membrane potential and the spike threshold, the stronger the static output nonlinearity imposed by the threshold. This is because only the most optimal stimuli will provide enough excitatory input to result in a spike. Weak suboptimal stimuli will result only in subthreshold responses. Because LGN firing rates in kittens are lower than those in the adult (Daniels et al. 1978), there are presumably lower baseline membrane potentials in kitten simple cells due to reduced excitatory input. If this is the case, it could result in the relatively stronger nonlinearities we observed in kittens compared with adult simple cells. The higher firing rates in adult LGN neurons could provide enough excitatory feedforward input, even for suboptimal stimuli, to elevate the
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simple cell membrane potential to close to the spike threshold and maintain the cell in a relatively more linear domain. Note that the actual membrane potential of the spike threshold in this scenario is the same for adults and kittens; it is only the baseline voltage that is different. Theoretical studies have described the relationship between membrane potential and threshold nonlinearities in detail (Hansel and van Vreeswijk 2002; Miller and Troyer 2002).

For the moment, it should be noted that because our RF maps are derived from extracellular measurements, they may be subject to the effects of spike thresholds (Bringuier et al. 1999). However, whereas the predicted orientation tuning bandwidths presented here and those predicted from intracellular RFs (Lampl et al. 2001) are similar, measured tuning bandwidths are much broader for intracellular responses. This suggests that spike thresholds have minimal effects on RFs generated on the basis of linear spatial summation.

In conclusion, our current results show that nonlinear mechanisms, presumably of cortical origin, participate substantially in the maturation and refinement of orientation tuning in young kittens. This process may be described quantitatively as one involving expansive nonlinearities. Once maturation is attained, orientation tuning appears to be correlated more clearly with linear RF elements.

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DISCLOSURES

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