The Development of Vernier Acuity in the Cat

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The development of vernier acuity was assessed in nine kittens using offsets in a series of square-wave gratings as stimulus targets. The kittens were tested on a jumping stand in a two-choice simultaneous discrimination paradigm, and daily thresholds were tracked with a modified staircase procedure. Vernier acuity improved gradually from initial values of 13-57 arc and reached asymptote at 1.5-5.4 arc by 70-90 days of age. The developmental function for vernier acuity is discussed in relation to physiologic development of the kitten visual system and is related to published data on the development of stereoacuity and spatial resolution in the same species. Invest Ophthalmol Vis Sci 31:1175-1180, 1990

Vernier acuity is a measure of the smallest misalignment detectable in a visual stimulus. In human adults, this ability is considered a hyperacuity because it is an order of magnitude better than the spatial resolution of the visual system as defined by sampling theory based on the foveal cone mosaic.1,2 The development of vernier acuity has been the subject of a number of investigations in human infants.3-5 The developmental time course of vernier acuity is much steeper than that of spatial resolution (grating acuity),3,5,6 but it parallels the development of stereoacuity,7,8 which is also a hyperacuity in human adults.2 In infants, vernier acuity is already superior to grating acuity by 4 months of age, and its superiority increases dramatically during the following weeks.3,3 However, Shimojo and Held5 reported that before 3 months of age vernier acuity is worse than grating acuity.

Most of the currently available data on vernier thresholds in nonhuman species come from studies of the cat.9-11 Adult cats achieve vernier thresholds that may also be considered hyperacuities in that they exceed both the behaviorally measured spatial resolution limit and the spacing of β-ganglion cells by up to a factor of three (see Ref. 11 for a full discussion of this point). It would be of considerable interest to know whether the same developmental relationship exists among vernier, stereo, and grating acuity in the cat as was outlined above in the human. Developmental data already exist for both stereoacuity12 and spatial resolution.13-15 The current study was undertaken to investigate the development of vernier acuity in kittens using a series of offsets in high-contrast square-wave gratings. Some of these data have appeared previously in abstract form.16

Materials and Methods

Vernier acuity was followed developmentally in nine kittens, some of which were littermates (litter 1: MK83, MK85, MK86; litter 2: MK87, MK88, MK89; litter 3: MK93, MK94; litter 4: MK96). Kittens were kept with their mothers and littermates until weaning. They then were housed individually and provided with food and water ad libitum. This research adhered to the ARVO Resolution on the Use of Animals in Research.

Behavioral training was initiated when the kittens were between 33 and 51 days of age (Table 1). The procedure used was a modification of the jumping-stand procedure developed by Mitchell et al.13 to measure resolution acuity in kittens, and used by Timney12 to study the development of stereoacuity in the same species. Kittens were trained to jump from a platform onto one of two stimuli placed on lockable trapdoors. Correct choices were rewarded with commercial beef baby food, and errors were punished by releasing the trapdoor and letting the kitten fall 40 cm onto a foam surface.

The vernier task is difficult for cats to learn.9,11 In order to minimize the number of trials required to reach criterion on the discrimination task, a fading-in technique was used (see Fig. 1 for a schematic illustration of the stimuli). The goal of this technique was to attract the attention of the kittens toward the middle portion of the stimulus, where the offset was located. A wide (1.2-cm) jagged line was superimposed on the middle portion of a very-low-contrast grating...
Table 1. Schedule of training and threshold measurement

<table>
<thead>
<tr>
<th>Cat</th>
<th>Age at onset of training (days)</th>
<th>Age at onset of threshold testing (days)</th>
<th>Age at asymptote (days)</th>
<th>Final threshold (min of arc)</th>
</tr>
</thead>
<tbody>
<tr>
<td>MK83</td>
<td>47</td>
<td>66</td>
<td>70</td>
<td>5.4</td>
</tr>
<tr>
<td>MK85</td>
<td>47</td>
<td>67</td>
<td>76</td>
<td>4.6</td>
</tr>
<tr>
<td>MK86</td>
<td>47</td>
<td>58</td>
<td>74</td>
<td>1.5</td>
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<tr>
<td>MK87</td>
<td>41</td>
<td>49</td>
<td>78</td>
<td>3.5</td>
</tr>
<tr>
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<td>41</td>
<td>51</td>
<td>74</td>
<td>3.8</td>
</tr>
<tr>
<td>MK89</td>
<td>41</td>
<td>60</td>
<td>83</td>
<td>4.4</td>
</tr>
<tr>
<td>MK93</td>
<td>51</td>
<td>62</td>
<td>87</td>
<td>3.1</td>
</tr>
<tr>
<td>MK94</td>
<td>51</td>
<td>55</td>
<td>90</td>
<td>5.2</td>
</tr>
<tr>
<td>MK96</td>
<td>33</td>
<td>46</td>
<td>83</td>
<td>4.0</td>
</tr>
</tbody>
</table>

(Fig. 1A). The positive stimulus was the grating with the jagged line, and the negative stimulus was a similar grating without jagged line (or offset). The contrast \( \frac{L_{\text{max}} - L_{\text{min}}}{L_{\text{max}} + L_{\text{min}}} \) of the first grating pair was 0.24. Grating spatial frequency ranged from 0.2–0.4 cyc/deg depending on the viewing distance, which was increased gradually during training. Once a kitten had mastered this problem (27/30 choices correct), the contrast of the gratings was increased to 0.48 and finally to 0.90 (Fig. 1B, C). The jagged line then was replaced by a large vernier offset (1.1° at 40-cm viewing distance; Fig. 1D). Animals usually transferred easily from the jagged line grating to the offset grating. Once the transfer was achieved, daily threshold measurements were initiated. The first threshold measurements were made when the kittens were between 46 and 67 days of age (Table 1).

Thresholds were delineated with a series of vertically oriented square-wave gratings that were generated by computer on a laser printer. Each stimulus subtended a total area of 27° × 21°. The offset sizes ranged from 49.5° arc (7.2 mm) to 1.1° arc (0.16 mm) in gradually decreasing step sizes (1° arc step between each of the nine smallest offsets). All measurements in visual angle are given for a 50-cm viewing distance, since most of our threshold measurements were done from this distance. Thresholds were determined daily using a modified version of the staircase procedure, the goal of which was to maximize the number of trials at near-threshold values. Stimuli were presented in order of decreasing offset size. Larger offsets were presented in two-trial blocks (2/2 choices correct required to proceed to the next smaller offset). Offsets within 1 octave of threshold (determined from the

Fig. 1. Schematic illustration (grey levels simulated by dot density) of the sequence of positive stimuli used in the fading-in training procedure. The goal of the procedure was to teach the kittens to respond to the presence of a highly salient marker (the jagged line—contrast 0.9) in the position where the vernier offsets would eventually appear. The carrier square-wave grating was gradually "faded in" by increasing its contrast from 0.24 (A) to 0.48 (B) and then to 0.9 (C). Finally, the jagged line was replaced by a vernier offset (D). For every step in the sequence, the negative stimulus was a square-wave grating of identical contrast to the positive stimulus. Kittens were trained to criterion (27/30 correct) on each stimulus in sequence.
previous day's performance) were presented in five-trial blocks (4/5 correct criterion). This ensured that the animals experienced easily detectable offsets every day, but also that they were brought rapidly to within 1 octave of threshold, where most of the data were collected. Inability to meet the appropriate criterion on a stimulus produced a three-step increase in offset size. This procedure was continued until several reversals of the staircase had occurred within the session. Viewing distance remained constant at 40 cm until the animal's performance approached the limits of our stimulus set, at which point viewing distance was increased to 50 cm. This occurred between days 70 and 82. This modification produced only a minor increase in the spatial frequency of the stimuli (0.34 to 0.44 c/deg).

Daily testing sessions consisted of a minimum of 40 trials, but in some cases more trials were required to reach a stable threshold. Daily thresholds were determined from the resulting frequency-of-seeing curves by joining the points and interpolating the vernier offset size that yielded 70% correct performance. Testing was continued until an animal's daily thresholds had reached asymptote. For one kitten (MK96), testing was continued for several weeks beyond this point (to 151 days of age).

**Results**

Figure 2A–C depicts the individual developmental functions for vernier thresholds in the nine subjects. At the earliest ages for which threshold measurements could be made in the kittens (46–67 days), performance was quite variable and thresholds ranged from 57 to 13' arc. Performance improved gradually over the following weeks and leveled off at values of 1.5–6' arc between 70 and 90 days of age. No evidence of a positive correlation was found between the age at which the task was mastered and threshold measurements begun, and the age at which asymptotic performance was achieved ($r = -0.24$, $P > 0.05$), suggesting that the threshold improvements...
measured were not simply a practice effect. The developmental function for vernier offset detection is summarized in Figure 2D, which plots median thresholds for the cats against age.

Kittens were tested for an average of 17 days (range 9-34) after their performance had reached a stable level. However, in order to be certain that no further improvement would occur with prolonged practice, one kitten (MK96) was tested until 151 days of age (69 days after asymptotic performance was reached). There was no evidence of late improvement in this animal. Its thresholds over the final days of testing (4–5' arc) were no better than those plotted out to 120 days of age (Fig. 2C).

The individual kittens' daily thresholds were somewhat variable because they were based on a rather small number of trials. However, once performance had stabilized at asymptote, it was possible to calculate cumulative frequency-of-seeing curves based on a large number of trials (100–130) per stimulus value near threshold. Final threshold values were determined individually for each animal by fitting a straight line by regression analysis to the descending portion of the frequency-of-seeing curve (Fig. 3). The interpolated offset size corresponding to 70% correct performance was taken as the kitten's threshold. The final estimated thresholds were found to range from 1.5 to 5.4' (Table 1). This range is consistent with the range of values reported previously in normal adult animals under equivalent testing conditions.1

Discussion

Even using the fading-in procedure, the vernier task required a considerable period of training. Therefore, it was impossible to determine thresholds with our technique prior to 46 days of age. After this time, however, rapid improvement was seen, with performance reaching asymptote at approximately 80 days of age. We believe that this improvement reflected real changes in visual function and was not simply a consequence of practice, since there was no positive correlation between the age at which threshold measurement was initiated in individual kittens and the age at which asymptotic performance was reached.

The range of final thresholds obtained here does not differ from those we have reported elsewhere11 for adult cats using three different stimulus configurations: the same 0.4 cyc/deg grating, a 1.1 cyc/deg grating, and a single line 16' arc wide. We cannot rule out the possibility that developmental studies using narrowly band-limited stimuli in different spatial frequency ranges might reveal slightly different time courses, reflecting the development of particular spatially tuned channels in the visual system. However, we would expect the final thresholds to be comparable to ours, at least over the midportion of the cat's contrast sensitivity function. By analogy to existing human data,17,18 one might expect a threshold drop-off for spatial frequencies at either extreme.

The developmental function described here closely resembles Timney's findings on stereovision development in kittens, which also shows rapid development leveling off around 80 days.12 These two functions differ markedly from the pattern of development seen for grating acuity,13–15 which shows a more gradual improvement, not reaching adult levels until over 100 days of age. It should be noted that although vernier acuity is a hyperacuity in adult cats, our vernier measurements at 60 days of age fall well below published values for grating acuity measured on the jumping stand in kittens of the same age.13,15 This pattern of much steeper developmental functions for vernier and stereo than for grating acuity has also been noted in human infants3 (although the human...
studies have not followed subjects to asymptotic adult levels of performance). Explanations at both peripheral\cite{19} and cortical\cite{20} levels have been proposed.

The cat clearly offers a valuable model for assessing these possibilities. Unfortunately, many existing studies of the anatomic and electrophysiologic development of the cat’s visual system are limited either to the first 4–5 postnatal weeks or to portions of the visual field representation peripheral to the area centralis. Since both human psychophysical studies\cite{21} and lesion data in the cat (Belleville and Wilkinson, unpublished observations) point to the central retina as supporting optimal vernier thresholds, and since in the cat there is a marked central-to-peripheral gradient in development (at least in the retina),\cite{22-26} we limit our discussion below wherever possible to studies explicitly examining the area centralis and its central projections.

The kitten’s optical media are clear by 28 days of age, and optical quality is well developed by 35 days.\cite{27,28} Although neurogenesis is still ongoing in the peripheral retina at birth, all neural components of the central retina are present, and area centralis maturation proceeds rapidly over the first 3 postnatal weeks.\cite{29-31} By 3 weeks, adultlike synaptic configurations are present at all retinal levels,\cite{24,30} and both alpha and beta cells in the area centralis achieve adult soma size and dendritic field spread.\cite{26,32} Rod and cone outer segments at the area centralis attain maturity by the end of the 5th week.\cite{29,30} While rod density undergoes a marked decline over the first 3–4 weeks, cone density (measured at the temporal rim of the area centralis) shows little change.\cite{33} This is in marked contrast to the late increase in central cone density in the human retina as the fovea is formed.\cite{34}

Electrophysiologically, the major components of the electoretinogram develop fully by 7 weeks,\cite{35,36} although there is further slow change in the implicit latency until 12 weeks and in the oscillatory potential until at least 18 weeks of age.\cite{36} Ganglion cells with both X- and Y-type response characteristics are found in the retina as early as 3 weeks, although the relative proportion of the two types varies over the next few weeks.\cite{37} Receptive field properties such as receptive field center (angular) size and strength of the inhibitory surround approach adult values by 7–12 weeks.\cite{37,38} Since retinal X-cells in adult cats have been reported to have displacement thresholds in the hyperacuity range,\cite{39} it would be valuable to have detailed developmental information about this property of ganglion cells.

The only gross structural change at the periphery that spans the period of vernier acuity improvement is eye growth. As the globe expands, the retina increases in size, apparently both by stretching and by active growth.\cite{31,32} However, the expansion is not uniform, and in fact very little change occurs in the central region of the retina.\cite{40} Consequently, as the posterior nodal distance increases, a smaller area of space is imaged on the same retinal area.\cite{41,42} This change in image magnification on the retina is presumed to make a significant contribution to the gradual decrease in ganglion cell receptive field dimensions\cite{37,38} and to the behaviorally assessed improvement in grating acuity which occurs over the first 3–4 months of life.\cite{13-15} However, this change is gradual and continues well beyond 80 postnatal days,\cite{41,42} the age at which our vernier measurements reached asymptote.

Striate cortex has been strongly implicated in the processing of vernier targets in the cat,\cite{9,10} and filters resembling striate simple cell receptive fields have been used in recent models for vernier acuity.\cite{18,43} The relevant properties of striate neurons from the point of view of these models are orientation and spatial frequency tuning, two properties which show significant changes during the early weeks of life in the kitten. Adultlike orientation bandwidths by 5–6 weeks have been reported by Bonds\cite{44}; spatial frequency bandwidths in the adult range by 5–7 weeks have been reported by Derrington and Fuchs,\cite{45} although it should be noted that receptive fields in this latter study lay outside the area centralis. The contrast sensitivity of cortical cells also was found to reach close to adult levels over the same period.\cite{45} On the other hand, the full range of optimal spatial frequencies was not achieved over the 12 weeks covered by the study; neurons tuned to the highest spatial frequencies seen in the adult were still lacking.\cite{45} A comparable finding for neuronal cut-off spatial frequency (neural grating acuity) has been reported for the lateral geniculate nucleus.\cite{46} Cortical synaptic density and number of synapses/neuron peaked at 70 days\cite{47}; after this age, a marked drop occurred in the number of asymmetric axo-spinous synapses (presumably excitatory); asymmetric axo-dendritic synapses remained stable after 70 days; and symmetric axodendritic synapses (presumed inhibitory) continued to increase until at least 110 days.\cite{47} Thus, the period during which vernier acuity develops is marked by refinement in cortical tuning and in the balance of excitatory and inhibitory influences.

Swindale and Cynader\cite{43,48} have reported recently that cortical neurons show marked sensitivity to the presence of vernier offsets. The development of offset tuning in striate neurons has yet to be examined. A close correlation between the development of this property of cortical receptive fields and the behavioral development reported in the current study would greatly strengthen the argument that these
cortical cells provide the neural substrate for vernier acuity.

Key words: vernier acuity, development, hyperacuity, cat, spatial resolution

References