STUDIES OF VERNIER ACUITY IN THE CAT

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SHORT TITLE

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ABSTRACT

This study investigated cat vernier acuity with a two-choice jumping-stand paradigm. In Experiment 1, vernier acuity was measured in normal adult cats using three types of stimulus targets. In normal cats, vernier acuity was 3-5', about two times better than resolution acuity. Experiment 2 reports pre- and post-operative vernier thresholds in cats which had sustained lesions of areas 17-18 in adulthood. The observed deficit confirmed the involvment of striate cortex in vernier acuity. The normal development of vernier acuity was investigated in Experiment 3. Vernier acuity developed rapidly from initial values of about 40' at 46 days to 2-5' at about 85 days. Experiments 4 and 5 examined the effect of neonatal removal of areas 17-18 on the development of vernier acuity and on resolution acuity. Whereas resolution acuity remained relatively normal, vernier acuity was severely disturbed. This confirms that the functional plasticity that follows neonatal cortical lesions is task-specific.

RESUME

Cette étude examine l'acuité vernier du chat à l'aide d'un appareil "Jumping-Stand". L'expérience 1 mesure l'acuité vernier de chats adultes normaux avec trois types de stimuli. Les seuils d'acuité sont de 3-5', environ 2 fois meilleurs que le seuil de résolution du chat. L'expérience 2 mesure l'effet de lésions adultes des aires 17-18 sur l'acuité vernier. Les déficits observés confirment l'implication du cortex strié dans l'acuité vernier. L'expérience 3 examine le développement normal de l'acuité vernier. L'acuité vernier se développe rapidement et atteint des seuils de 2-5' vers 85 jours. Les expériences 4 et 5 examinent l'effet de lesions périnatales des aires 17-18 ou 17-18-19 sur le développement de l'acuité vernier et sur l'acuité de résolution. Alors que l'acuité de résolution demeure relativement normale, l'acuité vernier est sévèrement déficiente. Ces résultats confirment que la plasticité fonctionnelle qui suit une lésion corticale périnatale dépend de la tâche.

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I would also like to thank the research assistants Margie Pathimos, Ellen Cytrynbaum and Davina Mill for their technical assistance throughout this research project along with Dr. Steven Zucker and Dr. Yvan Leclerc for producing the stimuli and Dr. Franco Lepore who performed the lesions in the adult cats. I also express my gratitude to Valter Ciocca and Ellen Cytrynbaum for their patience in proofreading this manuscript.

Finally, thank you also to my family and friends for their constant emotional support during these years.

PREFACE

The elements which should be considered original in my thesis are the following: the measurement of vernier acuity in normal adult cats using vertical square-wave grating as stimulus targets; the measurement of vernier acuity in normal developing kittens; the measurement of both the development of vernier acuity and resolution acuity in kittens which sustained early removal of the visual cortex (areas 17-18 and 17-18-19).

Assistance has been provided by Dr. Steven Zucker and Dr. Yvan Leclerc for the production of the stimuli; Davina Mill, Margie Pathimos, and Ellen Cytrynbaum assisted in testing the cats. Dr. Franco Lepore from the Department of Psychology of Universite de Montreal performed the adult lesions.

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CHAPTER 1

The visual capability of vertebrates and the structural organization of their visual system is adapted to the ambient illumination of their habitat. The trade-off of visual sensitivity (the ability to detect a light) and visual acuity (the ability to see fine details) characterizes nocturnal and diurnal species differently (Ali and Klyne, 1985). Nocturnal species operate under very low levels of illumination and their visual systems are organized in a way that emphasizes sensitivity. The cost to an organization that increases sensitivity is reduced spatial acuity. Diurnal species typically have visual systems that do not operate well under very low levels of illumination but exhibit particularly good ability to resolve fine spatial details. Most species cannot be classified as stricly diurnal or strictly nocturnal but possess visual adaptations that enable them to operate under a wide range of illumination conditions. Mixed cone-rod retina, concentration of cones in a fovea, quick adaptation mechanisms, and large eyes equipped with slit pupils are examples of adaptive features which allow activities by day and by night. Two examples of species well adapted to a large illumination range are humans and cats, the species that will be the main focus of discussion in this thesis. If they were to be placed on a continuum with strictly

nocturnal and strictly diurnal species at the extremities, cats would stand closer to the nocturnal end, and humans closer to the diurnal end of the scale. Nevertheless, these species share a fair number of adaptive features for diurnal vision and for this reason, the cat provides an interesting comparison to human vision. The two species are well equipped to operate under a wide range of illumination and their capacity in terms of acuity and sensitivity ought to reflect their light habit.

Vernier acuity, the ability to detect a misalignment of two line segments, is frequently put forward as an example of the fine capacity of the human photopic system. Vernier acuity has been widely investigated in the human species and several hypotheses have been put forward to explain its extreme precision (see Barlow, 1979a; Crick, Marr and Poggio, 1981; Watt, 1984b). However, little is known about its physiological substrate and few studies have examined this visual ability in species other than humans. The studies presented in this thesis investigate various aspects of vernier acuity in the cat. Measurements of vernier acuity thresholds in normal adult cats will be reported as well as the developmental pattern of vernier acuity in neurally intact kittens and in kittens which sustained an early removal of the visual cortex. The vernier acuity threshold of these cats will then be compared to their performance on another visual acuity task: resolution acuity.

Resolution acuity

One important characteristic of any visual system is that there is a limit to its capacity for resolving fine spatial details. If a spatially periodic pattern of lines (grating) is made gradually finer, a point will be reached beyond which it will not be differentiated from a uniform grey field. This represents the limit of the system's ability to separate features and has been labelled resolution acuity. In humans, the smallest angular separation at which two bars are perceived as separated is 30 seconds of arc.

Optical Factors

The limit to the ability for resolving spatial details has been related to the smearing imposed on the image by the optical system of the human eye, particularly by the interface between the air and the cornea and by the lens. The point-spread function, the degradation of a point by optical factors, is the most elementary way of describing the performance of an optical system since any image can be regarded as made up of an assembly of points (Westheimer, 1972). The image of each object point is diffused into the shape of the point-spread function and the final light distribution at each point in the image is the sum of the height of the **point-spread function (PSF)** of all object points (Westheimer, 1972). The procedure of summing the contribution of all target points weighted by a distance-dependent factor is called convolution. The **line-spread function** is the same optical degradation imposed on a line of an

infinitesimal width. The **modulation transfer function (MTF)** is the Fourier transform of a line-spread function. In order to go from an object to the image, the light distribution can either be convolved with the PSF (a summation process) or multiplied with the MTF. The MTF of the eye can be determined empirically by measuring the optical degradation of sinusoidal gratings of various spatial frequency, providing an index of the degradation imposed on each of them by the optical system. Campbell and Gubisch (1966) showed that under optimal conditions the highest spatial frequency passed through the optics of the human eye (the MTF cutoff) is 50-60 cycles per degree (c/deg) of visual angle. Therefore, the optics of the eye act as a band-limiting factor by removing all frequencies above 60 c/deg and attenuating lower ones by differing amounts, depending on the frequency. The MTF cutoff is the upper limit to visual resolution physically imposed by the optics and is in practice very close to behavioural measurements. The information eliminated by the optical system is irretrievable and therefore sets a limit to the visibility of details. However, the optics are probably not the only limiting factor to spatial resolution. It is possible to produce gratings on the retina that are finer than the 60 c/deg cutoff. By using coherent light to produce interference fringes, one can bypass the optics and produce gratings of any size directly on the retina. When the optics are bypassed in this manner, the resolution capacity of the visual system remains about 60 c/deg (Campbell and Green, 1965; Westheimer, 1960). Furthermore, there is a rapid decrease in resolution acuity just outside the fovea

which can not be explained by a concomitant decline in the optical quality. It therefore appears that there are limits to resolution beyond purely optical factors.

Photoreceptor Sampling

A second limit to resolution acuity is imposed by the mosaic of photoreceptors which transduces the image. Images falling on the retina have a smooth light distribution but are sampled by a discrete set of photoreceptors. For the image function to be accurately reconstructed from this discrete sample set, the optimal center-to-center spacing of the photoreceptors should be equivalent to the Nyquist limit (Bracewell, 1965; Oppenheim and Willsky, 1980). The Nyquist limit is half the period of the highest spatial frequency present in the image. In the case of the human visual system, the Nyquist limit is 30 seconds of arc, that is half the size of a period in a grating of 60 c/deg. This is the highest spatial frequency that is passed through the optics. Note that this is true when photoreceptors are packed in a square array, but as Snyder and Miller (1977) pointed out, in a hexagonal array similar to the human retina (Hirsch and Hylton, 1984), receptor spacing of $1/\sigma 3$ the highest spatial frequency would be sufficient. The center to center spacing of photoreceptors at the human fovea is 26-29 seconds of arc (calculated from Polyak's data (1941) by Yellott, Wandell and Cornsweet, 1984). This provides an excellent match to the information made available by the optical system. A coarser sampling would cause a loss of information (as is probably the

case in the periphery) whereas a finer sampling would be superfluous as it would not reveal any additional information. It is noteworthy that there is a one-to-one connectivity between the primate foveal cones and ganglion cells via the midget bipolar system (Boycott and Dowling, 1969; Kolb, 1970; Polyack, 1941). The absence of one-to-one connectivity in the human periphery, and in the central retina of many species, is probably responsible for the reduction of behaviourally measured resolution acuity below the level theoretically permitted by optics and receptor mosaic.

Resolution Acuity in Cats

In humans, foveal photoreceptors and ganglion-cell matrices are closely matched to the optical quality of the image. In cats, the photoreceptor matrix matches the optical image quality but the ganglion cell distribution does not. The behavioural cut-off spatial frequency is more closely related to the theoretical ganglion-cell cut-off frequency than to the optical quality.

The optical resolving power varies with pupil size (Enroth-Cugell and Robson, 1974; Robson and Enroth-Cugell, 1978) but, when the illumination conditions are optimal, the highest spatial frequency passed through the optics of the cat eye reaches 20 c/deg (Robson and Enroth-Cugell, 1978). On this basis, the maximum intercone distance for the image to be fully reconstructed would be about 1.5 minutes of arc. In the region of peak cone density (area centralis) the cone center-to-center spacing is 1.7' (Steinberg, Reid and Lacy, 1973), which closely

matches the resolving power. The exact cut-off spatial frequency predicted from the cone mosaic of cats is 17-18 c/deg. Although the optical resolving power of the cat eye approximately matches the cone mosaic, behaviourally measured resolution acuity falls well below this common limit.

When measured behaviourally (Blake, Cool and Crawford, 1974; Elberger, 1982; Jacobson, Franklin and McDonald, 1976; Mitchell, Giffin and Timney, 1977; Muir and Mitchell, 1975; Pasternak and Merigan, 1981; Smith, 1936) and by evoked potentials (Berkley and Watkins, 1973; Campbell, Maffei and Piccolino, 1973; Harris, 1978) the range of resolution acuity values of the cat visual system extends from 3 c/deg to over 10 c/deg. It is not clear why such a wide range of resolution acuity values are observed in cats but there are a number of factors (luminance, pupil size, total stimulus area, motivational conditions, threshold definition) to which it might be related. It is nevertheless clear that the optics and photoreceptor sampling are not the limiting factors to the behaviourally measured resolution acuity of cats.

In cats, unlike humans, a high degree of convergence occurs between the cone mosaic and the ganglion cells (Hughes, 1975; Steinberg, Reid and Lacy, 1973; Stone, 1965; Wassle, Boycott and Illing, 1981). Since the limit to resolution acuity is not set by the optical resolving power or by the cone mosaic, the possibility that it is related to the ganglion cells has been suggested. The interpretation of ganglion cell densities is however complicated by their classification into several classes,

two of which (X and Y cells) can be further subdivided into ON-centre and OFF-centre groups. The X-cells are probably involved in fine spatial analysis. ON and OFF beta cells (the morphological correlate of X-cells) form independent grids of equal density. Cell pairs from each grid are highly correlated (Wassle et al., 1981) which is suggestive of a simultaneous sampling of the same location by the two channels. On this basis, the spatial resolution of the visual system would be determined by the minimum interganglion cell spacing in one of the two maps. Wassle et al. (1981) calculated this distance to be 5.4' of arc, which would support a behavioural resolution acuity of 5-6 c/deg. There are suggestions that these grids do not operate independently (Hughes, 1981), in which case thresholds up to 10 c/deg could be supported (inter-ganglion cell distance of about 3'). In conclusion, the ganglion cells impose the peripheral limit on resolution acuity in cats, but a clear estimate of this limit (5 c/deg vs. 10 c/deg) depends on the interaction of ON- and OFF- grids of ganglion cells.

Hyperacuity

The limits imposed on resolution acuity are relatively well understood and have roots both in physical optics and photoreceptor sampling. There are other classes of acuity the limit to which exceeds either the resolution capability of the optical system or the photoreceptor topography. A large number of

studies have examined the underlying spatial and temporal properties of these acuity tasks. Westheimer (1975) emphasized the fact that many visual tasks exhibit this extraordinary accuracy and grouped them under the single classification of **hyperacuities.** Hyperacuity thresholds are obtained on a wide range of misalignment detection tasks: abutting lines or lines separated by gaps of differing size (vernier acuity), pairs of dots, bright or dark bars, squares, edges, a line and a chevron or three dots (see Figure 1) are all hyperacuities (Andrews, Butcher and Buckley, 1973; Ludvigh, 1953; Sullivan, Oatley and Sutherland, 1972; Westheimer and McKee, 1977b). This robustness to variation in stimulus configuration indicates that the exact nature of the stimulus is not a critical factor in these alignment tasks (Westheimer, 1979; Westheimer and McKee, 1977b). Thresholds for a variety of other tasks, which do not require an alignment judgement, are also in the hyperacuity range: stereoacuity, orientation judgement, curvature analysis, chevron analysis, spatial interval acuity (judgment on the size of the interval) and spatial frequency comparison (see Figure 2); (Berry, 1948; Hirsch and Hylton, 1982; Watt, 1984b; Watt and Andrews, 1982; Westheimer and McKee, 1977b). Apart from stereoacuity, these tasks all require that the observer performs a judgement of relative position (in a broad sense) in a two-dimensional plane. In the following section, the spatial properties of two-dimensional alignment tasks are discussed. Stereoacuity, which concerns position in three dimensions, will

FIGURE 1. Misalignment detection tasks. A: abutting lines. B: Lines with a gap. C: Two dots. D: Bright bars. E: Dark bars. F: Squares. G: Edges. H: A line and a chevron. I.: Three dots.

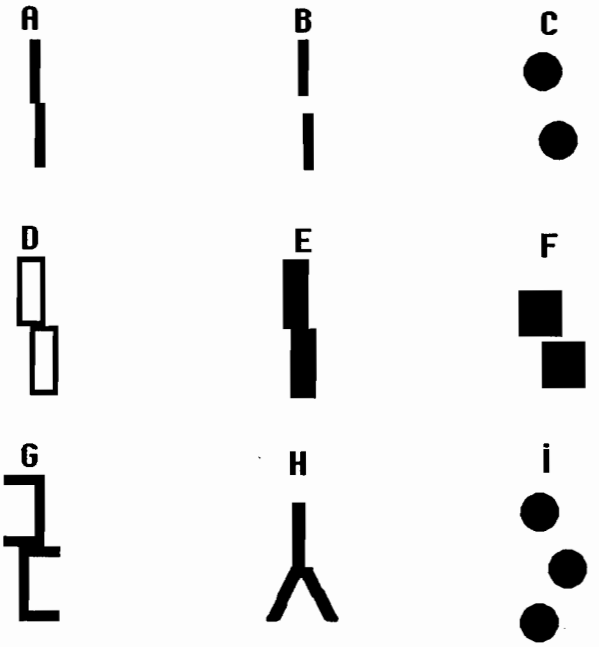
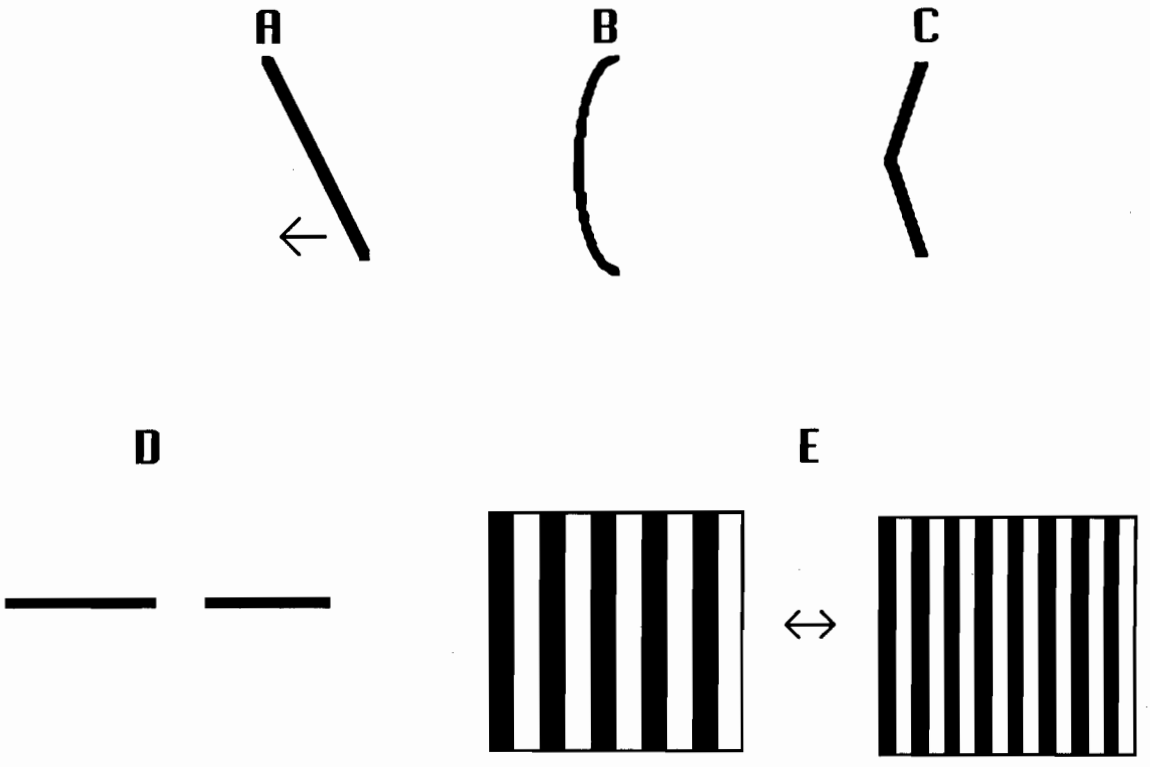


FIGURE 2. Other hyperacuity tasks. A: Orientation judgment. B: Curvature analysis. C: Chevron analysis. D: Spatial interval analysis. E: Spatial frequency comparison.



be more specifically discussed in a separate section later in the chapter.

Wulfing (1892) was the first to measure how small a horizontal misalignment a human observer could detect. He first noticed that previous researchers had always measured the capacity to judge the distance between two parallel lines, i.e. lines placed laterally one beside each other. He thought that the high thresholds obtained in such cases were due to irradiation in the retina and that the irradiation effect could be cancelled by using lines placed one above each other (vernier offsets). He found that practiced human observers could detect vernier offsets with a surprising accuracy. Vernier offsets as small as 3" of arc could be perceived. At that time, anatomists already agreed on the dimensions of the photoreceptors and Wulfing concluded that vernier thresholds were a fraction of the diameter of a cone.

Averaging Along the Length Hypothesis

Hering (1899) was the first to try to give an account of why the minimum detectable offset was so much smaller than a single retinal receptor. Because Wulfing had used line targets, Hering suggested that the underlying mechanism involved averaging local positional values (local signs) along the length of the stimulus. Hering's mean local sign theory was accepted by a number of experimenters who later studied vernier acuity (Andersen and Weymouth, 1923; Weymouth, Hines, Acres, Raaf and Wheeler 1928). Averill and Weymouth (1920) investigated the effect of varying the spatial properties of the stimulus on vernier thresholds to

clarify the conditions under which they hold. They measured vernier thresholds in abutting lines and showed no variation with increasing line width (a result later confirmed by Stigmar, 1970 and Sullivan et al., 1972), but an improvement of performance with line length up to 30' of arc. These data were consistent with Hering's averaging along the length hypothesis. Averaging over time was also suggested because short presentation duration seemed to increase vernier thresholds (Andersen and Weymouth, 1923). However, the threshold improvement with presentation time was later shown to be an effect of increased luminance rather than to reflect a mechanism that averages over time (Hadani, Meiri and Guri, 1984). Furthermore, contrary to Averill and Weymouth (1920), French (1920) found that the threshold improvement which occured with increasing line length disappeared beyond 4' of arc. It was also shown that, provided a gap was present between the two offset parts of the stimuli, two-dot alignment thresholds and vernier thresholds for small squares (1' long) were as good as vernier thresholds for 21 ' long lines (Ludvigh, 1953; Sullivan et al., 1972; Westheimer, 1979; Westheimer and McKee, 1977b). The contradictory data on the effect of line length and the fact that alignment acuity is comparable for stimuli devoided of vertical edges (e.g. dots) challenged Hering's hypothesis of a mechanism that averages over the length of the stimulus. French (1920) suggested that vernier acuity did not involve averaging along the length (mean local sign theory) as was proposed by Hering but was similar to an orientation judgement. Subjects were performing a task of

orientation judgement on the overall stimulus by a process similar to the fitting of a regression line to the outer ends of the two segments and the evaluation of the slope of the resulting line (global orientation hypothesis).

The Global Orientation Hypothesis

The idea that an alignment task is similar to one of orientation judgement on the whole stimulus has been and is still very prominent. However, many empirical data suggest that this cannot be the only mechanism involved in these alignment tasks. Similar hyperacuity thresholds are reported with stimuli that have contradictory orientation information (line and a chevron, Figure 1) or that are devoided of any discrete contour information (Westheimer, 1979; Westheimer and McKee, 1977a). Blur (ground glass blur) has a more detrimental effect on two-dot alignment than on line orientation acuity (Williams, Enoch and Essock, 1984) which would not be expected if both reflect the same mechanism (Williams et al., 1984).

The Local Orientation Hypothesis

A local orientation mechanism was later proposed (Sullivan et al., 1972) based on the effect of various gap sizes on alignment threshold (see Figure 1). Berry (1948) first investigated the effect of gap size on vernier acuity with long lines (about 80' long). He found a detrimental effect when gap size was larger than 2' of arc (Berry, 1948). A similar detrimental effect was reported with gap size larger than 5' of

arc in line stimuli (Andrews et al., 1973; Westheimer and McKee, 1977b), dots (Bech and Halloran, 1985; Beck and Schwartz, 1979; Sullivan et al., 1972) and short line segments (9' long) (Stigmar, 1970). At shorter gap sizes, thresholds remained relatively constant (Westheimer and McKee, 1977b). Sullivan et al. (1972) suggested that performance is based on a judgement of the orientation of the inner ends of the stimulus segments (local orientation hypothesis) rather than on the overall orientation (global orientation hypothesis). This implies that an imaginary line is fitted between the two offset parts separated by the gap and that, as separation increases, a larger displacement is required to produce a given angle of tilt. However, local orientation can not be the only mechanism used since hyperacuity thresholds are reached with abutting stimuli and since performance starts to decline only after a separation of 5'.

The relative steadiness of the threshold as gap size increases up to a 5' separation has been given other interpretations which do not require the existence of a single local orientation mechanism. Westheimer and McKee (1977b) explain this phenomenon by suggesting that the area surrounding the stimulus (about 5' large) is treated as a single unit by the visual system. On the other hand, Beck and Holloran (1985) proposed a dual mechanism: when the gap is below a given size (5') offset may be detected by a spatial comparison process that compares directly the position of the two stimulus-segments. Beyond a 5' separation, position can no longer be directly compared and offset is detected by discrimination of orientation

(the local orientation mechanism discussed above); (Beck and Holloran, 1985).

The Multi-Mechanisms Approach

Andrews et al. (1973) first suggested that different mechanisms may underlie different hyperacuity tasks. They compared thresholds for curvature acuity, chevron acuity, vernier acuity with and without gap, and slope acuity (see figures 1 and 2). They found line slope judgement optimal for stimulus size below 10' of arc whereas for vernier acuity, chevron acuity, three-dashes alignment and curvature analysis thresholds improved up to 30' length. Gap size up to 4' of arc had no effect on vernier performance for the long line stimuli used by Andrews et al. (1973), but larger gaps were detrimental. Slope sensitivity was found not to be good enough for slope cues to be used in any of these tasks, especially for long stimuli (Andrews et al., 1973). Furthermore, contrary to the idea that curvature analysis might be based on orientation analysis (through orientation units), chevron analysis (which uses a stimulus more adequate for orientation units) was not better than curvature analysis (Figure 2). Andrews and collaborators proposed two coding operations: an orientation coding which operates over small areas and which is involved in orientation acuity, and a "collinearity failure detector" concerned with curvature, chevron, and vernier acuity. Both mechanisms would be coded with the same efficiency by the visual system and would have access to a common pool of high grade information.

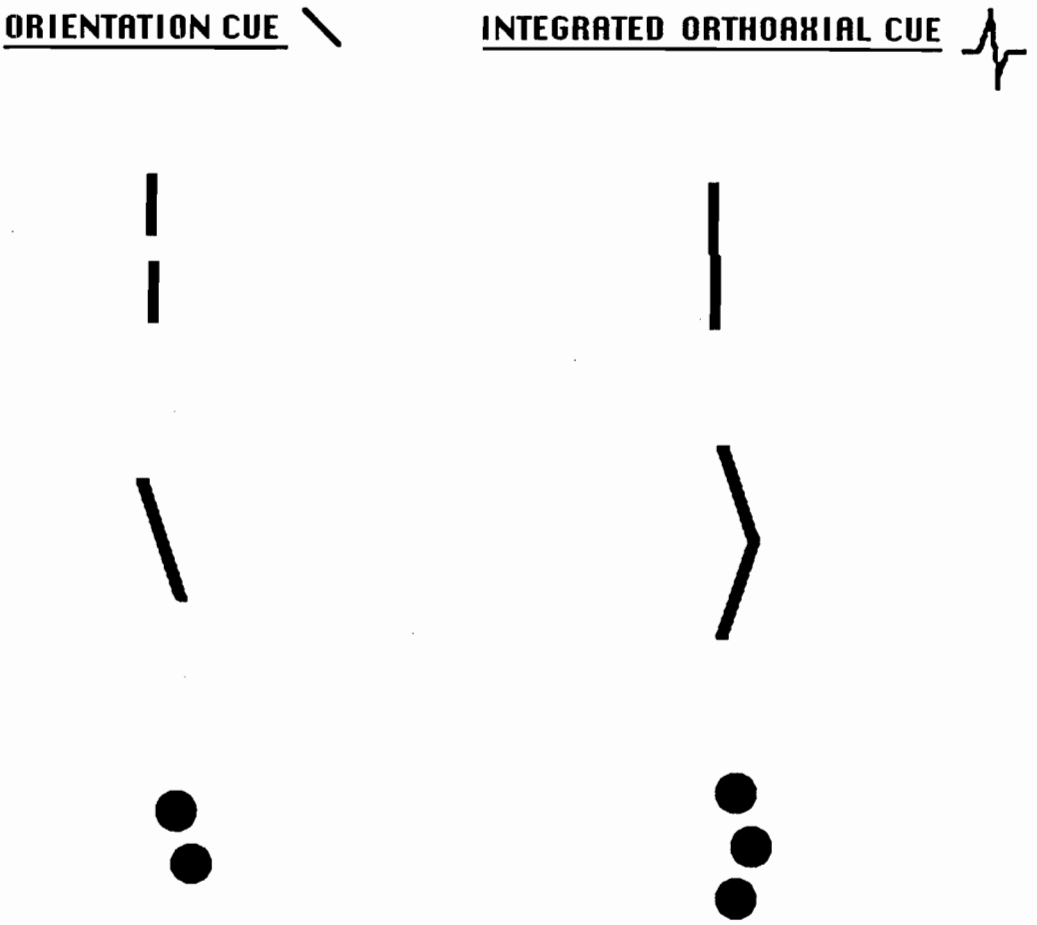
Watt and Andrews (1982) furthered the idea of two different mechanisms. One would analyze position across the axis of the target in a limited region of space. This type of information, which they called orthoaxial, would be collected and combined over a range of about 30' and would detect collinearity failure (Ward, Watt and Morgan, 1984; Watt, Morgan and Ward, 1983). A second mechanism would be a position and slope analyser that would provide slope and curvature comparison (Watt and Andrew, 1982; Watt 1984a; Watt et al., 1983a). Varying the slope of a vernier target made up of abutting lines showed no effect on vernier thresholds when the offset corners were sharp. In this type of stimulus, according to the authors, relative position information is left intact because the offset corners are sharp, but the orientation information is no longer available since the target is given a random slope on each trial (Ward et al., 1984, Watt et al, 1983). On the other hand, degrading the offset corners of the stimuli had a large detrimental effect but this effect levelled off at 10" when slope was fixed. In this case, orientation cues are available but not position information. When slope was randomized, that is neither orientation nor position information were available, log threshold increased linearly with amount of blur (Ward et al., 1984, Watt et al., 1983). Therefore, in a vernier task using abutting lines, orientation information can be used when the relative position information is not available. In normal conditions however, relative position information is predominant. These data are interesting because they generalize the hypothesis of different tasks reflecting

different mechanisms to a single task presented under different conditions.

Watt (1984b) extended the concept of different mechanisms involved in hyperacuity tasks. He examined and compared performance on various kinds of hyperacuity tasks as a function of their length and of gap size. When thresholds were reexpressed in terms of both slope orientation cues and magnitude of the integrated orthoaxial position cue, some tasks were well accounted for by slope information: vernier acuity for targets with a gap, slope acuity and two dot acuity (Figure 3). On the other hand, the data for vernier acuity with abutting lines, chevron acuity and three dot acuity (Figure 3) were better accounted for by an integrated orthoaxial cue. It is however probable, as suggested by Beck and Holloran (1985), that for separated stimuli in which gap size is below 5', offsets are detected by a direct comparison process rather than a slope analyser. Another mechanism was suggested to be involved in curvature analysis. Watt (1984b) did not mention stereoacuity, another hyperacuity which is likely to be governed by rules different from the previously mentioned tasks (see below) and related to a separate mechanism.

Orthoaxial information and curvature analysis have similar properties, they integrate information across space (30' arc), they do not suffer contour breaks in most circumstances (Andrews et al, 1973; Watt, 1984b; Watt and Andrews, 1982), and are therefore probably subject to contour segmentation restrictions and rules (Watt, 1984b). On the other hand, the slope mechanism

FIGURE 3. Tasks that are well accounted by slope information and tasks that are better accounted by an integrated orthoaxial cue.



does not collect information across space and is unaffected by contour segmentation. Watt (1984b) suggested that the first two (orthoaxial and curvature) were involved in contour shape while the third (slope mechanism) would analyse the spatial relations amongst the features of a figure.

Interference Effect

Hyperacuity is subject to crowding and interference. Hyperacuity thresholds are degraded if unrelated interfering stimuli are placed 2 to 5' in the vicinity of the target (Badcock and Westheimer, 1985; Westheimer and Hauske, 1975; Westheimer, Shimamura and McKee, 1976). If the interfering target is placed nearer or farther, the interaction is reduced. The interocular transfer of this interfering effect and its occurence in dichoptic presentations suggests a central locus for the neural processing subserving hyperacuity (Westheimer 1981; Westheimer and Hauske, 1975).

For Westheimer (1979) and Westheimer and McKee (1977a), the above experiments suggest that patches of the visual field covering a few minutes of arc (2' to 6') are subserved by their own processing network. Hence, a small area extending about 2-6' around the target is considered a single unit by the visual system. The process of determining a precise location requires the use of an unencumbered zone that extends a few minutes of arc around the stimulus. The same mechanism was suggested to be responsible for the absence of gap size effect below 5'. This series of experiments places restrictions on the underlying

mechanisms: they should operate optimally for distances in the range of 2-6' and can not be critically dependent on the nature of the stimulus.

Effect of Retinal Eccentricity and Blur

The effects of retinal eccentricity and blur on hyperacuity have been relatively well documented. These investigations are relevant because they help in differentiating whether the limits of hyperacuity are a reflection of optical factors or neural sampling factors. Experiments on the effect of blur also shed some light on the involvement of spatial frequency mechanisms in hyperacuity.

There is a rapid decrease in some alignment acuities (step displacement and vernier acuity) just outside the fovea (Legrand, 1967; Westheimer, 1979, 1982). At 5^{o} eccentricity, step displacement acuity is about 20" of arc and it is about 60" of arc at 10^{o} eccentricity, compared to 6" at fovea (Westheimer, 1982). The fall-off of step displacement acuity with retinal eccentricity is more rapid than that of resolution acuity (Westheimer, 1982). This rapid fall-off might depend on the decrease in neural sampling with eccentricity. Beck and Holloran (1985) investigated two-dot acuity in relation to increasing eccentricity and vertical separation (gap size). For a constant dot separation, eccentricity had no significant effect on two-dot acuity in one subject and caused only a slight (about 20%) increase from 4 to 8 degrees eccentricity in another subject (Beck and Holloran, 1985). This supported the idea that two-dot

acuity was based on a judgment of the slope of the virtual line joining the two dots and not on a direct comparison of the position of each dot. Indeed, an orientation mechanism is less likely to be affected by a decrease in cone sampling. Beck and Holloran conclude that this orientation mechanism is probably a function of a central process relatively little affected by the sampling differences between the fovea and the periphery. The difference in the effect of retinal eccentricity upon vernier and two-dot alignment supports the hypothesis of different mechanisms involved. However, it should be noted that the two-dot acuity thresholds reported by Beck and Holloran were particularly poor at all eccentricities (30" to almost 500").

If the band of spatial frequencies admitted to the retina is altered with filters (Stigmar, 1971), ground glass (Williams et al., 1984) or spectacle blur (Westheimer, 1979), resolution acuity is, as expected, very much affected, but alignment acuity is not. Alignment thresholds are slightly affected (30% decrease) when the image is severely degraded (1.0 diopter) but even in the presence of considerable amounts of blur, performance remains in the hyperacuity range (Westheimer, 1979). The relative superiority of abutting lines over stimuli in which test details are widely separated was shown to disappear with blur (Stigmar, 1971; Williams et al., 1984). In fact, the presence of a gap of increasing size (8-24') as blur increases facilitates location of the stimuli (Stigmar, 1971; Williams et al., 1984). In line orientation judgement, shorter lines (below 8') were more affected by blur than ones above 16' (Williams et al., 1984). If

two-dot alignment and orientation acuity reflect similar mechanisms, as suggested by Watt (1984), the length effect on blurred line orientation judgement might be related to the increased optimum gap size found in blurred two-dot alignment.

It therefore appears that, whereas the sharpness of the retinal image is a prerequisite for resolution acuity, this condition can be somewhat relaxed for alignment acuities. The blurring function acts essentially as a low-pass filter by removing all higher spatial frequencies. Therefore, the visual process responsible for the hyperacuity response in alignment tasks does not depend upon the integrity of spatial frequencies that are above 2-10 c/d and can generate a relatively precise localization response when only low spatial frequencies are present (Williams et al., 1984).

The difference in robustness to blur between resolution and alignment acuities might be used as an illustration of their distinct character. The ability to resolve two points of light is dependent upon the quality of the optical system and might be viewed as a function concerned with the analysis of the nature of features. On the other hand, alignment acuities may reflect processes involved in the location of a feature and its relation with other objects. This localization seems to be possible with low-contrast blurred visual stimuli.

Spatio-Temporal Properties

A number of investigators have shown alignment acuities to be particularly resistant to variations of their temporal properties.

Temporal summation in vernier acuity depends on luminance level. However, if enough light is provided in a 10-20 msec period, thresholds are almost normal. This means that the neural signal resulting from this instantaneous exposure contains sufficient information for hyperacuity (Westheimer, 1981).

Simultaneous presentation of the two offset parts yields optimal performance in hyperacuity tasks (Westheimer, 1981; Westheimer and Hauske, 1975). However, a 20msec simultaneous exposure appears sufficient to produce hyperacuity thresholds and a sequential presentation (within specific conditions) still yields thresholds in the hyperacuity range (Burr, 1979; Westheimer and Hauske, 1975).

Certain experiments indicate that retinal stimuli can be integrated over a certain spatial and temporal region to yield a local signal precise enough to participate in a hyperacuity judgement. Hyperacuity is robust to movement of the stimuli on the retina (Westheimer, 1979, 1981; Westheimer and McKee, 1975). In a 200 msec presentation when no tracking eye movement is possible, a vernier target can move at a 2^{o}/sec velocity without affecting performance (Fahle and Poggio, 1981; Westheimer, 1979, 1981; Westheimer and McKee, 1975). This means that a subject can detect the relative position of two lines to within a fraction of the receptor diameter while the whole pattern moves across 30

receptors in 200 msec. A low luminance vernier target briefly presented produces high thresholds but, if the same target is flashed repeatedly for 200 msec, performance is returned to a hyperacuity level by a process of summation of the flashing input. These stimuli do not need to be presented at the same retinal location and can be swept over a 2-4' arc area while flashing (Westheimer, 1981; Westheimer and McKee, 1977b). When a target is swept over a 2-4' arc area in a ten-flash presentation (20 msec), the perceived target will not be the single flash but the sum of the whole configuration (the ten flashes). The vernier offset extracted will be the result of the sum of the offset information contained in each single flash (Westheimer, 1981; Westheimer and McKee, 1977b). Apparent vernier offset can be created by using stroboscopic presentations of aligned bars (Burr, 1979; Burr and Ross, 1986; Fahle and Poggio, 1981; Morgan and Watt, 1982). The offset is produced by introducing a delay between the presentation of the lower and upper part of a stroboscopically flashed stimulus. The stimuli are presented at 7 stations creating an apparent moving offset and the upper segment is displayed 10 msec before the lower. Under these conditions, performance remains in the hyperacuity range (about 11" of arc, just slightly higher than the threshold for a real spatial offset). These findings had a considerable impact on understanding hyperacuities because they require that the visual system interpolate the positional information between the discrete stations.

Stereoacuity

Because of their different positions in the head, each eye receives a different image of an external stimulus. The difference in position of the same image point on each retina is called retinal disparity and is a strong depth cue because it varies with distance. Stereoacuity is the smallest difference in depth that can be perceived between two targets based on disparity information. Stereoacuity thresholds of 2-6" of arc have been reported (Andersen and Weymouth, 1923; Berry, 1948; Bourdon, 1900; Howard, 1919; Stigmar, 1970; Westheimer, 1979; Westheimer and McKee, 1979; Woodburne, 1934) which are well within the hyperacuity range. Similarities exist between stereoacuity and other hyperacuities. Stereoacuity, like alignment acuities, is optimal under simultaneous presentation of the two segment targets (Westheimer, 1979, 1981), is subject to crowding and interference (Butler and Westheimer, 1978) and tolerates low-velocity movement of the stimuli on the retina (Westheimer and McKee, 1978).

Stereoacuity was initially proposed to be based on the binocular fusion of two separate monocular vernier judgements (Stratton, 1898). Therefore, the evaluation of feature separation in each eye would precede stereoacuity. This idea has been challenged by many observations on vernier acuity and stereoacuities. No difference was found in vernier acuity thresholds whether measured binocularly or monocularly suggesting no binocular summation (Berry, 1948; Stigmar, 1970). It has also been shown that stereoacuity thresholds were too good to be

accounted for by a simple summation of two separate vernier targets (Berry, 1948; Stigmar, 1970; Westheimer, 1981). Stereo-vernier targets were used to study stereoacuity and vernier acuity under similar conditions. In the stereo-vernier situation, the target is separately projected to each eye so that the offset direction can be independently varied. In the vernier situation, each monocular offset has the same direction; in the stereo situation, the offset projected to each eye has opposite direction in order to produce a stereoscopic effect. Stereoacuity and vernier acuity are then separately evaluated. Stereo-vernier thresholds were measured with typical vernier targets (Berry, 1948), but also with three-line alignment (Stigmar, 1970) and bisection tasks (Westheimer and McKee, 1979). Using this paradigm, stereoacuity was comparable to vernier thresholds. This would not be possible if it was the result of two monocular vernier judgement since the separation of each monocular stimulus at stereo-threshold is half that of the vernier threshold. Consequently, stereoacuity is too good to be based on the detection of an offset in each monocular segment (Berry, 1948; Stigmar, 1970; Westheimer, 1981; Westheimer and McKee, 1979). Rather, the monocular images are probably combined after which the disparity value is evaluated.

There is additional evidence suggesting that the mechanisms subserving stereoacuity differ from those subserving alignment acuity because they behave differently in response to variations in some of their spatial properties. Berry (1948) investigated the effect of a gap on stereo-vernier targets and found the two

types of acuity differently affected. Stereoacuity was more resistant to the presence of a gap between the two test details. The size of target separation that could be tolerated to maintain good stereoacuity thresholds was much larger (up to 30') than it was for vernier acuity (2-6') (Berry, 1948; Westheimer, 1981). Stigmar (1970) also reported an optimal vernier performance with abutting stimuli whereas stereo performance was best for separated stimuli and deteriorated with reducing gap size from an optimal size of 4-7' to about 2'.

Stigmar (1971) examined the effect of blur on both stereoacuity and vernier acuity. Little detrimental effect was found in either task. This finding has not been confirmed by Westheimer (1979) who reported a much more deleterious effect of spectacle blur on stereoacuity than on either resolution acuity or displacement acuity. It should be noted that the effect reported by Westheimer was produced with spectacle blur which does not act as a low-pass filter but alters the range of spatial frequency accessible to the visual system in a somewhat more complicated way (see Westheimer, 1979).

Despite the remaining uncertainties as to the effect of blur, enough dissimilarities characterize stereo and alignment acuities to suggest that they reflect different mechanisms. However, as was originally pointed out by Andrews et al. (1973), it is probable that stereoacuity has access to the same pool of very fine grade information which is subsequently processed differently from alignment acuities.

Interpolation Processes and Physiological Substrate

The extreme accuracy of hyperacuities compared to the relative coarseness of the receptor mosaic suggests that the visual system can interpolate between the discrete samples provided by the mosaic (Barlow, 1979a, b, 1981; Crick et al., 1981; Hirsch and Hylton, 1982; Morgan and Watt, 1982). In computational terms, it is theoretically possible for a function to be reconstructed with a better accuracy than sampling. The sampling theorem stipulates that given a continuous low-passed function, reconstruction is possible from a discrete set of samples (Bracewell, 1965; Oppenheim and Willsky, 1980). The optics of the eyes act as a low-pass filter by removing frequencies above 60 c/deg. The sample points then need to be convolved with a mathematical function, possibly the function sinc/c=sin(∏x)/∏x (Barlow, 1979a, b, 1981; Crick et al., 1981). Notice however that the sinc/c function probably requires too much spatial extent to be applied (Zucker and Hummel, 1986). Simpler mathematical functions (Laplacian or Gaussian) were shown to be as efficient as the sinc/c function (Crick et al., 1981; Zucker and Hummmel, 1986). These functions have been related to receptive fields of various sizes (Wilson, 1986; Zucker and Hummel, 1986). The information would be preserved in the visual pathway as zero-crossings, peaks or means (see below). Provided that the function is band-passed (i.e. both low and high frequency components are removed), single features such as zero-crossings are a rich source of information. The position

information on the retina could be processed by the visual system by encoding the location and occurrence of zero-crossings in the second derivative of the light distribution and then identified as edges (Watt and Morgan, 1983a). The receptive-fields of the ganglion cells are probably efficient band-pass mechanisms. Features would then be reconstructed on a fine scale in layer IVc of the visual cortex. Hence, the whole image need not be reconstructed as long as the single features (zero-crossing, peak or mean in the second derivative) are (Crick et al., 1981).

The interpolation hypothesis was supported by empirical evidence some of which has already been presented in the preceding sections (e.g. temporal properties). The interpolation hypothesis implies that information about position is not lost even if it is provided by discrete samples. Morgan and Watt (1982) empirically showed that such a task was possible. Hyperacuity thresholds (5-10") were measured using a misalignment in a sinusoidal luminance profile represented by a coarse sample of vertical bars with an inter-sample distance up to 150-200 seconds arc. A similar phenomenon was reported for stereoacuity (Morgan and Watt, 1982). A 2 msec exposure of small dot stimuli where image shift is not possible and averaging much reduced yielded hyperacuity thresholds (Hadani et al., 1984). Because a minimal number of cones would then be affected, performance can only be accounted for by an interpolation mechanism.

Located feature. An image contains a wide variety of information which can be used as the features upon which a localization process (such as interpolation) can be applied. The reconstructed feature might be the mean (centroid) of the light distribution, the peak, the edge threshold, or the zero-crossing (Barlow, 1979a; Crick et al., 1981; Watt and Morgan, 1983a). As pointed out by Watt and Morgan (1983b) the psychophysical data on various hyperacuity tasks strongly suggest that the visual system assigns location to the entire light distribution and not to isolated features such as peaks or edges. Zero-crossings and mean (centroid) are both features which require orthoaxial information and which, because they are not directly present in the image, require an interpolation process. A number of authors favour zero-crossings as the located feature in the case of a sharp edge (Barlow, 1979; Crick et al., 1981; Watt and Morgan, 1983b). However, some evidence suggests that aspects other than zero-crossings are used in location analysis and that localization is performed on the centroid of the light distribution of the stimuli to be compared (Badcock and Westheimer, 1985; Westheimer, 1981; Westheimer and McKee, 1977a). A misalignment between the center of gravity of the internal light distribution of two aligned stimuli was detected with the same accuracy as in a typical vernier acuity (Watt and Morgan, 1983a; Westheimer and McKee, 1977a). Furthermore, moving the centroid of a stimulus target by adding a flanking line on either side affects performance by "pulling" the perceived position toward the flanking line (Badcock and Westheimer, 1985). These

results suggest that the corner offset (zero-crossing) is not the only feature used in location analysis and that the centroid of the light distribution is also an important feature. The stationary points in the second derivative of the light distribution were also proposed to be the features detected and represented in a primitive map (Watt and Morgan, 1983b, 1984). The next stage following the elaboration of a primitive map would be contour grouping. The task of edge detection and contour and positional analysis would thus be combined (Watt and Morgan, 1983b).

Neurophysiological substrates. Specific characteristics of hyperacuity, its sensitivity to interfering contours and its resistance to motion and blur, suggest that hyperacuity depends upon an analysis derived from a pool of receptors and that the underlying mechanism resides in the central nervous system. However, despite sophisticated computational models, the actual neural implementation of hyperacuities is as yet little understood. As of now, few studies have investigated the possible neural substrates of hyperacuities.

The striate cortex was suggested as a likely location for an interpolation process to take place. The neural characteristics of layer IVcβ (the major target layer of the lateral genicualte nucleus (LGN) parvocellular laminae) appear suitable for a finely grained reconstruction (Barlow, 1979a,b, 1981; Crick, et al.; 1981, Fahle and Poggio, 1981). In primates, the cells in this layer have the same general receptive field structure as retinal

ganglion and geniculate cells (Blasdel and Fitzpatrick, 1984; Hubel and Wiesel, 1968, 1977) but are much more numerous (O'Kusky and Colonnier, 1982). These are properties that would be expected of cells involved in the reconstruction of the information encoded by the retinal-X cells.

Striate cortex has been implicated in the processing of vernier acuity in the cat. After removal of areas 17 and 18, only one of three cats was able to learn the vernier task and this animal's vernier threshold was 12 times worse than its preoperative acuity (Berkley and Sprague, 1979; Sprague et al., 1979). These cats were, however, only mildly impaired on a resolution acuity task (about 20% decrease in performace) (Berkley and Sprague, 1979; Sprague et al., 1979,). More recently, Berkley and Bush (1983) found impairments in vernier acuity after perpendicular slicing in area 17. They interpreted this as evidence of the involvement in vernier acuity of intra-cortical processing that takes place within the striate cortex.

Most authors agree on the implication of the striate cortex in processing hyperacuity (there are exceptions; see below). However, some do not agree on the necessity of an interpolation mechanism. Recently, Shapley and Victor (1986) reported that cats' X-retinal ganglion cells responded to the displacement of a grating by less than 3' of arc. A response to a small spatial displacement of a stimulus within the boundaries of the receptive field center of a cat retinal ganglion cell was also observed by Scobey and Horowitz (1972) and Sur and Sherman (1984).

Displacement acuity can be defined as a hyperacuity if it is better than 3-10' of arc, depending on which of resolution acuity values reported in the literature is used as a comparison (range: 3c/deg to 10c/deg. See above). In the case of Sur and Sherman and Scobey and Horowitz' report, the theoretical resolution capacity of the cell was known and the perception of a smaller spatial displacement implied some kind of "cell hyperacuity". Shapley and Victor (1986) postulate that hyperacuity can be achieved by simple linear filtering by the retina and that complex central processing need not be invoked. Note however, that there are examples of binocular hyperacuity localization (stereoacuity) tasks which have to be processed beyond the retina. Recording from the laminae A of the cat LGN showed that both X- and Y-cells respond to very small displacements of gratings (Moss and Lehmkuhle, 1986). At the highest spatial frequencies, X-cells' sensitivity is better than that of Y-cells, but it is identical (low spatial frequencies) or worse (medium spatial frequencies) at other spatial frequencies. It is important to note that all the preceding experiments used a displacement acuity paradigm: the stimulus was given a sudden change in position. Therefore, there was no spatial offset in their stimulus targets. Whether these moving displacement tasks involve the same mechanism as the classical static alignment tasks remains to be confirmed.

In another report, most simple and complex cells in cats' striate cortex had their response inhibited by the presence of a vernier offset in a bar swept across their receptive field (Swindale and Cynader, 1986). Interestingly, the same inhibitory

effect was produced if the bar was simply oriented in the same direction (Swindale and Cynader, 1986). The authors suggest that this is an indication that orientation and vernier acuity are behaviourally related. However, human psychophysical studies suggest that vernier acuity does not depend upon an orientation mechanism (Watt, 1984b; Watt et al., 1983). Whether this is also true for cats is not yet determined but if cat's vernier acuity is underlaid by a mechanism similar to that of humans, the effect reported here might reflect orientation preference rather than true vernier sensitivity.

Questions remain as to the role of spatial frequency and orientation mechanisms in hyperacuity. A model has been proposed to explain alignment acuities with orientation and size tuned mechanisms (Wilson, 1986). This model suggests that offsets are computed by pooling neighbouring units at all orientations and sizes. This model has been successfully applied to many human psychophysical data (vernier acuity, chevron acuity, curvature acuity), although some other data were not as easily accounted for by it (stimuli with large gap size). The model has however the advantage of demonstrating that information sufficient for alignment acuity is present in the spatial and size tuned mechanisms that exist in the human visual system.

Evoked potential (EP) recording has been carried out in human subjects under conditions that were similar to psychophysical testing (Zak and Berkley, 1986). Evoked responses were recorded when offsets were presented in horizontal and vertical vernier stimuli and in three-line alignment. Flanked

lines had a suppressive effect on EP amplitude confirming psychophysical data (Westheimer and Hauske, 1975). This implies that the vernier-elicited EP reflects the central processing that underlies vernier acuity. The long latency of the vernier elicited EP suggested to the authors that the site of the mechanism involved in fine spatial localization was outside the primary visual area (Zak and Berkley, 1986). This was also confirmed more recently by Srebro and Osentisky (1987) using a different stimulus target. However, latency is not necessarily a good localization predictor in evoked potential and the demonstrated implication of cat striate cortex in vernier acuity argues in favor of area 17 as a necessary preprocessor.

Hyperacuity in Non-Human Species

There are many reasons why the investigation of alignment acuity or other hyperacuities in non-human species is necessary. Phylogenetic comparisons of a behavioural function give insights as to the type of adaptation requirements that may lead to its development or to its refinement. Contrasting and comparing the performance of organisms that differ in some ways but are similar in others may certainly contribute to the understanding of the factors involved in a particular ability. In the case of hyperacuity, investigating performance in species in which neural factors differ from those encountered in humans might help in evaluating the extent to which the measured function depends upon these characteristics. In addition, the neural mechanism at the single cell level is only accessible in non-human species. The

contribution of single-cell recording studies to the understanding of vision has been enormous since Hubel and Wiesel's (1962) early report and it continues to provide new insights to understanding vision. As discussed above, single-cell recording has been done in cats using vernier offset and displacement stimuli. However, in order to interpret these data on single cells, it is essential to have behavioural measures in the same species to know how the whole system performs.

Little is known about hyperacuity in species other than humans. In primates, stereoacuity is the only type of hyperacuity for which thresholds have been reported. Stereoacuity thresholds of about 5" of arc have been reported in adult rhesus monkeys (Cowey and Wilkinson, in preparation but discussed in Cowey, 1985; Sarmiento, 1975). The monkey's performance was comparable to that of human observers in similar conditions and is in the hyperacuity range for primates (De Valois, Morgan and Snodderly, 1974). Stereoacuity has also been measured in normal cats for which thresholds were reported to range from 4' to 10' of arc disparity (Blake and Hirsch, 1975; Kaye, Mitchell and Cynader, 1981; Timney, 1981, 1983, 1984). The only published work which has examined alignment abilities in a non-human species has reported cats' vernier thresholds from 4' to 8' of arc (Berkley and Bush, 1981; Berkley and Sprague, 1979) when measured with a short line segment. In the first experiment of the present thesis, I extend the investigation of cat vernier acuity by measuring their performance using offsets in series of vertical square-wave gratings of two different spatial frequencies and in

single line stimuli. The second experiment was designed to confirm the involvement of striate cortex in cat vernier acuity. Vernier acuity thresholds were measured pre- and post-operatively in two adult cats which sustained removal of the part of visual area 17 that represents the central 5-10 degrees of the visual field.

Development of vernier acuity

The following section introduces what constitutes the rest of this research work on vernier acuity, namely its development in normal kittens and in kittens which sustained an early removal of the visual cortex.

The interest in developmental studies arose partly from the longstanding debate started by Hering and Helmholtz between nativists who believed that innate factors regulated human behaviour and empiricists who held that environmental factors were the critical ones. While the opposition between nativism and empiricism in visual perception has faded away, the interest in the developmental aspects of perception remains strong. Developmental studies provide valuable information about the nature of the physiological mechanisms underlying visual perception because such mechanisms develop in parallel with measurable behavioural functions. Moreover, the knowledge of the development of brain structures and of the corresponding behaviour may allow us to have a clearer insight into their possible organization and functioning at the final stage of development. For this reason, it was important to study the development of vernier acuity in normal kittens and in kittens which sustained a neonatal removal of the visual cortex. In the following pages, the development of normal acuity functions in

humans and the normal development of visual pathways and acuity functions in cats will be briefly summarized.

Normal Development of Acuity Functions in Humans

The development of human resolution acuity has been well documented (Birch, Gwiazda, Bauer, Naegele and Held, 1983; Dobson and Teller, 1978; Held, 1979; Mayer and Dobson, 1980; 1982; Norcia and Tyler, 1985; Sokol and Moskowitz, 1985; Van Hof-Van Duin, 1986). When measured behaviourally with the Forced-Preferential-Looking technique (FPL), children's resolution acuity develops gradually during the first six months of life from about 0.9 c/deg at 2 months, to about 12 c/deg at six months. A plateau is reached at that time and development slows down for about 5 months (Van Hof-Van Duin and Mohn, 1986). Extended measurement of resolution acuity showed that it reaches adult level around five years of age (Birch et al., 1983).

Resolution acuity estimated from the amplitude of visually evoked potentials (VEP) suggests higher estimates. Based on VEP amplitudes, resolution acuity is about 4.5 c/deg at 2.5 weeks and approaches adult values (30 c/d) at 6 months of age (Dobson and Teller, 1978; Norcia and Tyler, 1985). A number of factors have been related to the differences between behavioural and electrophysiological estimates of resolution acuity. The VEP represents some part of the visual cortex activity to visual stimulation. The presence of an evoked response indicates that the stimulus has been resolved up to that point in the visual pathway. An evoked potential threshold is estimated by

extrapolation from measurements and is based on the assumption that the evoked response declines linearly with spatial frequency increase near acuity threshold and depends on a measure that is sampled at sufficiently fine intervals (see Norcia and Tyler, 1985). It is however difficult to compare directly a VEP threshold based on such criteria to an acuity threshold based on a psychometric function. In addition, controversies exist as to whether amplitude or peak latency should be used as criteria for VEP acuity estimate. Traditionally, most authors have used amplitude to estimate the resolution acuity threshold from the evoked potential response. Recently, Sokol and Moskowitz (1985) reported that latency values correlate better than amplitude values with individual psychophysical estimates. Resolution acuity estimates based on latency values parallel those based on FPL technique. The main disadvantage of using latency is however the large inter-individual variability which therefore demands an extended analysis of individual data in order to estimate thresholds.

The development of stereoacuity has been measured with FPL and electrophysiological techniques which show remarkable agreement (Aslin and Dumais, 1980; Birch, Gwiazda and Held, 1985; Held, Birch and Gwiazda, 1980; Petrig, Julesz, Kropll, Baumgartner and Anliker, 1981). Stereoacuity improves very rapidly after the onset of stereopsis (about 2 months of age) and reaches 1' of arc around 5 months of age. Since smaller values have not been tested yet, we do not know when stereoacuity reaches hyperacuity values in children.

Only recently has the development of vernier acuity been investigated in human infants (Manny and Klein, 1984, 1985; Shimojo and Held, 1987; Shimojo, Birch, Gwiazda and Held, 1984). Vernier development has been studied using FPL but with two different types of stimulus targets. The FPL method classically used in infant research requires that the young children be visually attracted to the stimulus. In order to increase the attention of the children to the vernier offset, Shimojo and his colleagues used a dynamic vernier target in which the offset slowly moves along the stimulus length. Manny and Klein (1984, 1985) compared children's performance using either FPL with the moving target or with the classical vernier target in which the offset is static. The moving offset stimulus yielded slightly better thresholds than the static offset target. One hypothesis put forward to explain this difference is that the threshold performance with the moving target reflects both vernier acuity and apparent motion. Similarly, it is possible that the movement of an offset the size of which is too small to be perceived, produces flickering. Conversely, the moving target may simply enhance the attention of the infant at near threshold values. Until we have more information about infants' motion perception, both alternatives are possible. Mannie and Klein (1985) mention that in normal adults the difference in threshold is reversed and subjects judged the moving target more difficult to track.

Shimojo et al. (1984) report vernier thresholds of about 16' of arc at 2 months of age which improve to about 2.5' of arc at 6 months. Manny and Klein (1985) report thresholds around 30' of

arc at about two months of age which reach about 3' of arc around 6 months of age. Vernier acuity measured in 14 month old infants was still not better than 3' (Manny and Klein, 1985). Interestingly, the developmental time course of vernier acuity varies markedly from that of resolution acuity (Shimojo et al., 1984) but parallels the development of stereoacuity (Birch et al., 1982, 1985). The rate of development in both hyperacuities was found to be much steeper than that of resolution acuity. In human adults, vernier acuity and stereoacuity are hyperacuities because they are better than the spatial resolution of the system. In infants, vernier acuity is already superior to resolution acuity at 4 months of age and its superiority increases with age (vernier acuity is about 50% better at 4 months of age and 100% better at 6 months). However, before 3 months of age, vernier acuity is worse than resolution acuity (Shimojo and Held, 1987).

Normal Development of Visual Pathways in Cats

The development of behaviourally measured functions is closely related to the development of underlying neural processes. For this reason, before considering the behavioural development of acuity functions in cats, we will provide an overview of the normal development of their visual pathways.

Eye and retina. Generally, the visual system of the kitten is relatively immature at birth. Kittens are born with closed eyes that open around 8-10 days after birth. The size of the eye

slowly increases during the first 6 months of life. This slow increase in size is due to the longer development of the anterior chamber. The vitreous chamber reaches adult size earlier, around 12 weeks postnatal (Thorn, Gollender and Erickson, 1976). The optical media is clear by 28 days of age and the optical quality is well developed by 35 days (Bonds and Freeman, 1978; Thorn et al., 1976). This means that beyond 5 weeks of age the optical quality is not a limiting factor to the development of resolution acuity.

Three major periods of postnatal retinal development can be distinguished anatomically and physiologically (Hamasaki and Maguire, 1985; Vogel, 1978). The retina is quite immature at birth (Donovan, 1966; Vogel, 1978). A slow initial phase occurs in the first week of life during which the outer segment of the receptors and synapses start developing. A second main vigorous growth phase occurs from the 7th day of life to 30th day after which layering and the general retinal structure reach adult appearance. Then a third phase of slow intracellular differentiation terminates around 120 days of age. The maturation of photoreceptors occurs in a centripetal way, with those in the central region developing faster than those in periphery (Donovan, 1966; Vogel, 1978).

The ganglion cell layer is anatomically mature by about 18 days (Donovan, 1966). At 21 days, the ganglion cells already have a center-surround receptive field organization (Hamasaki and Flynn, 1977). In kittens, the response of ganglion cells to stimulation is weaker, the intensity curve flatter, the surround

very large and its inhibition weaker than in adults (Hamasaki and Flynn, 1977; Rusoff and Dubin, 1977). The angular dimensions of the receptive fields are larger in kittens than in adults but this is compensated for by a shorter focal length so that the extent of the receptive field on the retina is equivalent to that in adults (Hamasaki and Flynn, 1977). Therefore, dendritic arborization, if receptive field size is related to it, is already laid down (Hamasaki and Flynn, 1977). At 56 days postnatal, the angular receptive field center size is about that of adults (Hamasaki and Sutija, 1979). This considerable decrease in receptive field size is mainly due to eye growth (Hamasaki and Flynn, 1977; Rusoff and Dubin, 1977). Almost all the ganglion cells studied in kittens older than 28 days of age had adult-like properties except for a much larger, relatively unresponsive surround. The electroretinogram shows that connections in the inner-plexiform layer are probably not completely mature until 70-84 days of age which may contribute to the relative immaturity of ganglion cells (Hamasaki and Maguire, 1985).

At very early ages, most ganglion cells can not be easily classified as X- or Y-cells (Hamasaki and Sutija, 1979; Sherman, 1985). Note however that by 56 days postnatal, the percentage of X-cells is that of adults. It is generally agreed that the postnatal development of X- and Y-cells differs with Y-cells developing much more slowly than X-cells (Hamasaki and Sutija, 1979; Sherman, 1985).

Lateral geniculate nucleus. Anatomically, the LGN is immature at birth but reaches 2/3 of its adult size during the first post-natal month. Afterwards, the rate of growth declines markedly (Kalil, 1978). At birth (or shortly after birth), the segregation of the retinothalamic afferents is complete but not the laminar segregation (Shatz, 1983; Shatz and Kirkwood, 1984). Laminae develop around birth and differentiate until the 30th day of age (Kalil, 1978).

Physiologically, LGN cells of kittens younger than 21 days have low maintained rate, large receptive fields, absence of surround response and surround inhibition (Daniels, Pettigrew and Norman, 1978; Ikeda and Tremain, 1978). Like ganglion cells, LGN cells can not be easily classified as X- or Y-cells before 21 days and X-cells develop mature receptive field properties earlier (20 days) than Y-cells (later than 35 days) (Daniels et al., 1978, Tootle and Friedlander, 1986). A subgroup of Y-cells was suggested to develop faster (Friedlander, 1982). The development of the cells' spatial resolving power is probably very relevant to the development of resolution acuity in kittens. The spatial resolving power of cells in laminae A and A1 of the cat LGN develops gradually during the first 112 days of life from initial values of about 1 c/deg at 21 days to 3-4.75 c/deg at 112 days (Ikeda and Tremain, 1978).

Cortex. At the cortical level, the main afferent and efferent projections of the primary cortex are present at birth (Anker and Cragg, 1974; Henderson, 1982). During the perinatal

period intense synaptogenesis occurs and the number of synapses that characterizes adult level is reached at approximately 40 days (Cragg, 1972). Thalamic projections to area 18 come later by 14-21 days of age. Trans-cortical connections to area 19 and to areas in the lateral suprasylvian gyrus are present at approximately 20 days and callosal projections to the 17-18 borders at 40 days (Anker and Cragg, 1974).

At 8-15 days postnatal, there is no segregation of geniculocortical projections into discrete ocular dominance bands and most cells are binocular (Levay, Stryker and Shatz, 1978). In addition, the spatial arrangement of orientation selective neurons is very rudimentary (Albus and Wolf, 1984). In general, units in the immature cortex respond with few spikes of longer duration, their receptive fields are larger, and they are more difficult to classify (Levay et al., 1978). At early ages (14 days), most units are non-specific to orientation, direction, or disparity (Pettigrew, 1974). After eye opening, the number of orientation selective cells increases dramatically and is similar to that of adults by about 28 days (Albus and Wolf, 1984; Pettigrew, 1974). Direction and orientation specificity approaches adult levels around 35 days of age (Pettigrew, 1974). By 90 days of age, cells are well distributed into ocular dominance columns (Levay et al., 1978). The development of the resolving power of cortical units has not been investigated beyond 42 days (Derrington, 1977; Derrington and Fuch, 1981). Optimum spatial frequency and peak sensitivity increase with age while the size of the bandwidth decreases. At 42 days, the

resolving power of cortical units reaches 3 c/deg (Derrington, 1977).

Normal Development of Acuity Functions in Cats

At birth the visual system of the cat is relatively immature and most of its development occurs during the postnatal period. The fact that the development of the cat visual pathways occurs in the main part after birth makes it a particularly good model for the study of the development of visual functions.

In cats, the development of both resolution acuity (binocular and monocular) (Giffin and Mitchell, 1978; Mitchell et al., 1976; Mitchell et al., 1977; Sireteanu, 1985), and stereoacuity (Timney, 1981, 1983, 1984) has been measured behaviourally. In this species, these acuities develop at different rates and reach adult level at different ages. Resolution acuity develops gradually from initial values of about 0.1 c/deg around 21 days of age (Sireteanu, 1986) and reaches adult values around 120 days of age (Giffin and Mitchell, 1978; Mitchell et al., 1976; Mitchell, et al., 1977). When measured with evoked potentials, the development of resolution acuity reaches an asymptotic level of about 3 c/deg at 100 days (Freeman and Marg, 1975). The development of resolution acuity is probably related to the development of the spatial resolving power of geniculate neurons which attains adult values around 112 days (Ikeda and Treiman, 1978).

Stereoacuity improves rapidly after the onset of stereopsis (30-35 days of age). By 45-50 days postnatal, stereoacuity

reaches about 30' of arc. It then improves more gradually and reaches adult values (4' of arc) around 80 days (Timney, 1981, 1983, 1984). The development of stereoacuity was related to that of ocular dominance columns (Mitchell and Timney, 1982, 1984) which reach complete development around the same age (Levay et al., 1978). The development of vernier acuity in cats, on the other hand, has never been measured. Experiment 3 was undertaken to investigate the development of vernier acuity in normal kittens using a series of offsets in high-contrast square-wave gratings. A final objective of the present undertaking is to examine the development of vernier acuity in cats which sustained a neonatal removal of the visual cortex (Experiment 4) and to compare their performance on a resolution acuity task to their vernier acuity (Experiment 5).

CHAPTER 2

GENERAL METHOD

This chapter will provide a description of the methodological aspects common to the experiments that will be described in the following chapters: subject sample, apparatus, stimulus production and general training procedures. The specific details (psychophysical procedures, stimulus description, surgical and histological procedures) that pertain to each experiment will be included in the appropriate chapters.

Subjects

A total of 19 cats were used as subjects in this research. They were all bred in our laboratory except for subjects MK83 to MK89 which were provided by the department of Psychology of Queen's University. Kittens were kept with their mothers and littermates until weaning. They were then individually housed in metallic cages (77 cm wide, 77 cm long, 68 cm high) placed in a well ventilated room where a 12h-12h light/dark cycle was maintained. Animals were provided with food (Purina Chow) and water ad libitum. Some cats (MK68 and MK73) habitually ate all

their daily ration immediately upon receiving it. In order to prevent satiation prior to testing and to ensure that these cats would eat the food reward given during testing, their supplementary ration was provided after completion of the daily testing session. When possible, comparisons were made between kittens from the same litter in order to minimize interindividual differences. Table 1 gives the identification number, sex, and litter of each cat as well as the experiment for which it was a subject. Before they were used as subjects in this study, some cats (MK51, MK58, MK73, MK74) had had previous experience with the testing apparatus on unrelated tasks. However, their behaviour did not suggest any interference or facilitation effects.

The sequence of presentation of the experiments is not necessarily the sequence in which they were run. Some animals were used as subjects in more than one experiment (e.g.; subjects MK86 and MK88 were used in the developmental study and then in the adult lesion study). As a consequence, the presentation of a subject's results in an experiment may precede that of a second experiment even if they were actually done in the reverse order. The order of presentation was chosen to facilitate understanding of the underlying rationale and comparison between the experiments.

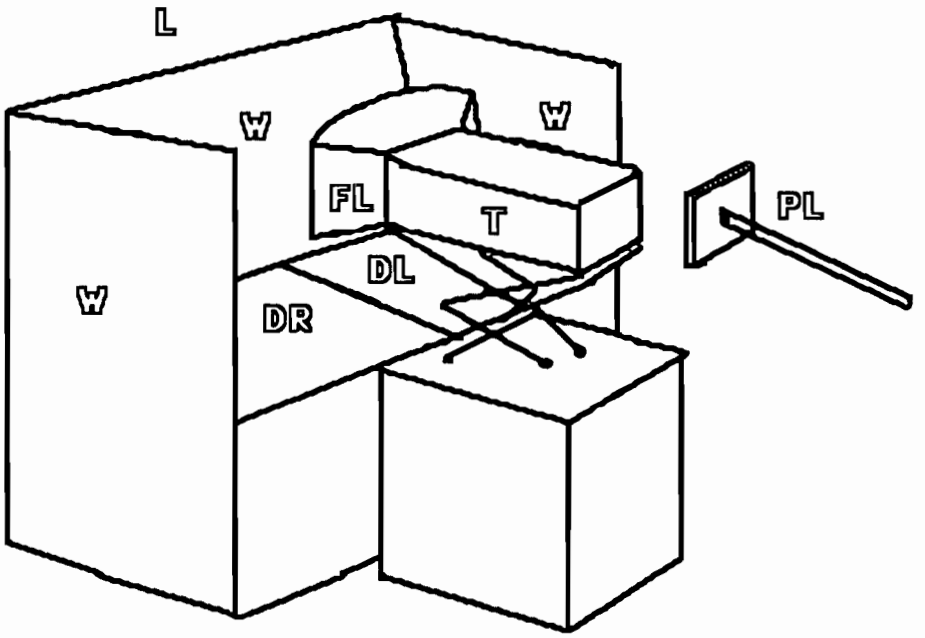
TABLE 1. This Table shows for each cat their sex, litter and experiments in which they were used as subjects.

CAT	SEX	LITTER	EXPERIMENT
MK58	FEMALE	1	1
MK68	FEMALE	2	1
MK73	FEMALE	3	4 & 5
MK74	FEMALE	3	5
MK78	MALE	4	1
MK79	MALE	4	1
MK80	MALE	4	1
MK83	FEMALE	5	3
MK85	FEMALE	5	3
MK86	FEMALE	5	2 & 3
MK87	MALE	6	3
MK88	FEMALE	6	2 & 3
MK89	FEMALE	6	3
MK91	FEMALE	7	4 & 5
MK92	MALE	7	4 & 5
MK93	FEMALE	7	3, 4 & 5
MK94	FEMALE	7	3, 4 & 5
MK95	MALE	8	4
MK96	FEMALE	8	3 & 4

Apparatus

All behavioural testing was carried out using a jumping stand similar to that first described by Mitchell et al. (1976). The apparatus consisted of a white rectangular wooden box 66 cm wide and 36 cm long. The stimuli were placed onto two lockable trapdoors (DR and DL in Figure 4) which could be released in order to let the cat fall a short distance down (45 cm) onto a foam surface. The trapdoors were surrounded by three walls 45 cm high that prevented the animal from being distracted by other aspects of the testing room or from escaping the apparatus (W in Figure 4). A tunnel (T in Figure 4) led to an enclosed platform the end of which coincided with the edge of the apparatus. The walls of the jumping platform (FL on Figure 4) were flared so that the experimenter positioned behind the animal could not see which stimulus the animal looked at (lateral head movements) but could see if the animal was leaning below the jumping platform. The tunnel was narrow enough to prevent the cat from turning around (12 cm wide). A smaller tunnel was used for kittens (9 cm wide). The tunnel and platform were placed on an adjustable jack which allowed rapid adjustment of the height. All testing was performed in a well-ventilated room lit with ordinary fluorescent or incandescent light. A desk light with an incandescent bulb placed behind the apparatus at a height of 50 cm provided additional illumination (see L on Figure 4 for the usual position of the light). The average luminance level measured at the

FIGURE 4. Diagram of the jumping stand apparatus used in the present set of studies.



stimuli was about 300 candelas/meter^2 (cd/m^2) when overhead fluorescent lights were used and about 140 cd/m^2 when overhead incandescent lights were used. This range of lighting condition is well within the photopic range and did not make any difference to the results.

Stimuli

The vernier stimuli were computer generated on a laser printer (LN01 laser printer) with a spatial resolution of 1/300 inch. The stimuli were produced by Dr. Y. Leclerc and Dr. S. Zucker from the Department of Engineering of McGill University. The stimuli were mounted individually on rigid white cardboard squares (35 cm by 35 cm) that covered the entire surface of the trapdoor bearing them. The stimuli were protected with washable transparent plastic (Mac-Tac) with a mat finish.

Two sets of photographically produced grating stimuli were used to measure resolution acuity. For the first set, stimuli were placed in a white holder that entirely covered the door bearing them (35 cm by 35 cm) and were covered with mat transparent plastic. The second set of stimuli was mounted on rigid cardboards (23 cm by 23 cm) the edges of which were covered with black tape (2 cm wide).

General procedure

Jumping-Stand Pre-Training

Before training on a discrimination task, animals were accustomed to the testing situation and taught to jump in the apparatus. They were first encouraged to step out from the tunnel onto one of the two doors using warm beef liver baby food as a reward. On the first day, the jumping platform was kept at the same height as the stimulus doors so that kittens were not required to jump and could easily walk from the tunnel onto the stimuli. One of the two doors was locked while the other was opened. The position of the closed door was pseudo-randomly varied. A similar procedure was used on the second and third day of the habituation phase but the height of the jumping platform was increased by 3 cm at the beginning of each testing session and to 15 cm on the fourth day. During this first stage we were careful to encourage and reassure the kittens after every trial because their subsequent behaviour on the jumping-stand is influenced by how they habituate to the testing situation.

In the study involving adults (Chapter 3) animals were first trained on a brightness discrimination task (White vs Black) in 40-trial daily sessions. The learning criterion was set to 90% correct performance over 30 consecutive trials. In the developmental studies (Chapter 5 and 6), it was important to start measuring thresholds as early as possible. In order to minimize training time, kittens tested developmentally were not

given the brightness discrimination task and were trained on the vernier task immediately after habituation to the apparatus.

Training Procedure

As a first step, the training procedure involved the discrimination of the positive stimulus from a negative stimulus. The positive stimulus was always a grating or a single line with a horizontal offset at its center and the negative stimulus was an identical grating or a single line without offset. The stimuli are described in more detail in the next chapters. Cats were tested in 40-trial daily sessions. The door bearing the positive stimulus was locked. If an animal responded appropriately, it was rewarded with a small amount of a preferred food (Heinz Beef Baby Food or Heinz Liver Baby Food). If, however, it jumped to the incorrect stimulus, the trap door was released and the cat fell a distance of 45 cm onto a soft foam surface. This reinforcement procedure was maintained during both initial training and threshold measurement.

Our prior experience with the apparatus showed that if the animal was permitted to delay in responding, its attention was distracted by other aspects of the apparatus. Consequently, the animals were allowed an initial 30 seconds period to respond and were then gently prodded at regular intervals using a flat wooden plunger which fit snuggly into the tunnel behind the cat (PL in Figure 4). The left-right position of the stimuli was varied according to a pseudo-random sequence. After every trial, the

stimuli were systematically moved in order to keep constant any auditory cues.

During the learning phase, the height of the jumping platform was gradually increased from an initial level of 30 cm to a final height of approximately 50 cm which then remained constant throughout threshold evaluation (see below). Thus, the viewing distance was always kept at or beyond the near point of accomodation (shortest distance at which appropriate accomodation to the stimulus is possible) for cats as measured by Bloom and Berkley (1977). During the initial learning period, we were very careful to prevent the animal from attempting to lean toward the stimuli before jumping. Cats that showed a tendency to lean were discouraged by placing the experimenter's hand just below the tunnel exit.

Viewing distance was monitored on a frequent basis throughout training and threshold delineation. In addition to monitoring done by the experimenters during testing, some of the sessions were videotaped. The position of the animal's eyes just prior to its jump was used to determine its viewing distance. This should be considered a conservative estimate as the animal may actually make its choice from a greater distance during its approach toward the edge of the jumping platform.

The learning criterion was set to a 90% correct performance on 30 consecutive trials. When animals were tested on more than one stimulus set (Experiment 1; see Chapter 3), they were retrained to this criterion on each subsequent task and received

additional practice trials before threshold assessment on each task.

CHAPTER 3

EXPERIMENT 1: VERNIER ACUITY IN THE NORMAL CAT

Vernier acuity has been extensively studied in human subjects. However, few studies report vernier acuity thresholds or consider the extent of hyperacuity in non-human species. The only published work to this effect reported vernier acuity in cats to range from 4' to 8' of arc (Berkley and Bush, 1983; Berkley and Sprague, 1979). Because their vernier acuity was not better than their resolution acuity, the authors concluded that cats, unlike humans, do not exhibit hyperacuity.

However, Berkley and Sprague (1979) used as stimulus targets offsets in a very short line segment (5^{o} long, 10' wide). This task may have lacked the salience necessary to elicit optimal performance from cats. The present study was undertaken to investigate more extensively vernier acuity of normal cats using testing conditions which differed in a number of respects from those of Berkley and Sprague (1979). The authors tested their cats in a testing box with nose pressing response under fairly low levels of luminance (44 cd/m^2). In the present study, vernier acuity was measured on the jumping-stand apparatus under higher luminance levels, using two different stimulus targets - single lines and gratings of two different spatial frequencies. We expected that the redundant nature of our grating stimuli would increase their salience and yield better performance in cats.

Method

Vernier Stimuli

To delineate vernier thresholds, animals were tested in a two-choice simultaneous discrimination task in which they had to choose the stimulus (grating or line) with a horizontal offset at its midpoint. Three stimulus sets were used: high contrast vertical square-wave gratings of two spatial frequencies (Grating 1: half-period of 10 mm; Grating 2: half-period of 4mm) and single vertical lines (2.4 mm wide and 195 mm long). Grating 1 stimuli contained 13 cycles and Grating 2 stimuli contained 29 cycles. The size of the offsets ranged from 7.2 mm to 0.16 mm. The number of offsets and the step sizes for each stimulus set are explicitly given in Appendix 1. For all subjects, threshold measurements were made from a viewing distance of 50 cm except for MK58 whose viewing distance was 47 cm. Appendix 1 gives angular measurements based on all the viewing distances used in the present study. The average contrast value was about 0.7.

Procedure

Vernier thresholds were measured in five normal adult cats, three of which were littermates. The general training and testing procedures were as described in Chapter 2. For each cat, the psychophysical procedure used and the order of testing on each stimulus set is indicated in Table 2. Since the vernier task is

TABLE 2. Training and testing histories for the five cats of experiment 1. CS: method of constant stimuli; SP: staircase procedure; G1: Grating 1 (.4 c/deg); G2: Grating 2 (1.1 c/deg); SL: single line.

CAT:	MK58	MK68	MK78	MK79	MK80
AGE (DAYS) AT ONSET OF TRAINING	92	45	65	65	150
TRIALS TO CRITERION	925	2661	1042	582	433
PRACTICE TRIALS	2070	3040	520	520	820
AGE (MONTHS) AT THRESHOLD MEASUREMENT	8-10	7-9	4-6	4-6	6-8
PSYCHOPHYSICAL PROCEDURE	SP & CS	CS	SP	SP	SP
STIMULUS ORDER	G1	G1-G2-SL	G1-G2-SL	G1-SL-G2	G1-SL-G2-G1-G1*

* This animal was retested on grating 1 from two different viewing distances (50 and 75 cm).

highly learning dependent in human subjects (Westheimer and Hauske, 1975), the animals were given a large number of practice trials on various offset sizes after reaching criterion and before the measurement of their vernier acuity (Table 2). Following this sequence of testing, one animal's (MK80) threshold on grating 1 was retested at the original height (50cm) and at a higher position (75cm) to confirm correct estimation of the position of the eyes in the first measure of the threshold.

Threshold Measurement

Two psychophysical procedures were used to delineate vernier threshold.

Modified staircase procedure. Within a 40-trial daily session, the stimuli were presented (one trial each) in order of decreasing offset until the animals failed to respond correctly. A failure produced an increase of four steps in the offset series (4-6' at 50 cm; see Appendix 1). This increase was followed by the presentation of the next stimulus in decreasing order of offset until the animal failed again. This was continued over the 40 trials. Animals were tested over a sufficient number of days to gather 50-130 trials at each near-threshold value.

Method of constant stimuli. From the performance of the animal on the practice trials and from previous data from other animals, 10 offset values were chosen to surround the threshold and were presented in random order. Four sets of 10 random presentations were given every day over a period of 20 days totalling 80 trials at each offset value.

Results

Table 2 gives the number of trials required to reach criterion for each normal cat. Trials to criterion range from 433 to 2661. The variation in number of trials to criterion probably reflects individual differences in learning ability, motivation, or attention. No significant relation was found between the number of trials to criterion and the threshold value.

In order to determine thresholds, a frequency of seeing curve was constructed from the performance of each cat on each stimulus set. Correct performance was plotted against offset size on a linear scale. The threshold was determined by fitting a straight line to each data set by regression analysis. We used as threshold the offset value that yielded a 70% correct performance based on the regression line. In fitting the regression line, only the data points in the descending portion of the curve were included in the analysis. The following criteria, illustrated in Figure 5, were used in defining the descending portion. Based on the animal's performance on the four largest offset values, a confidence interval (2 standard deviations) of asymptotic performance was determined and defined the upper limit. The smallest offset for which performance still fell within that

FIGURE 5. Example of the criteria used to determine the descending portion of the frequency of seeing curve. Filled arrow: the smallest value for which performance falls within the confidence interval. Open arrow: the largest stimulus for which performance is at chance level.

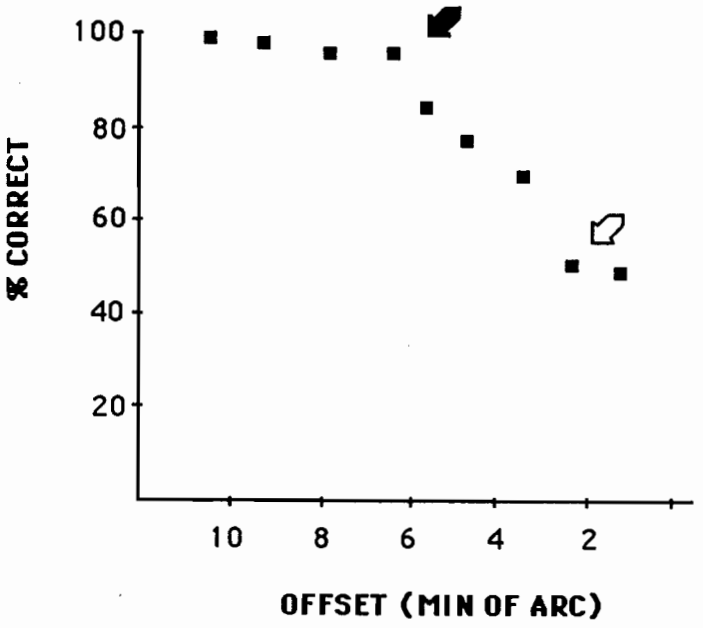


TABLE 3. Vernier acuity thresholds (70% cutoff criterion) for MK58 (a) and for MK68, MK78, MK79, MK80 (b). A second threshold estimate (60% cutoff) is given in brackets.

a.

	MK58	
	STAIRCASE	**CONSTANT STIMULI**
GRATING 1		
70% THRESHOLD	6.4'	6.7'
(60% CUTOFF)	(4.2')	(5.1')

b.

	MK68	**MK78**	**MK79**	**MK80**
GRATING 1				
70% THRESHOLD	5.4'	5.0'	3.3'	3.3'
(60% CUTOFF)	(4.2')	(4.1')	(2.6')	(2.7')
GRATING 2				
70% THRESHOLD	4.3'	3.3'	2.2'	2.6'
(60% CUTOFF)	(3.6')	(2.7')	(1.6')	(1.9')
SINGLE LINE				
70 % THRESHOLD	6.1'	3.1'	3.3'	4.6'
(60% CUTOFF)	(5.0')	(2.3')	(1.4')	(3.9')

range was taken as the top value of the curve (dark arrow in Figure 5). The smallest offset included in the analysis was the largest offset for which performance did not differ significantly from chance (0.05 confidence level) using the normal approximation to the binomial distribution (white arrow in Figure 5).

Cat MK58 was tested on Grating 1 with both the staircase procedure and the method of constant stimuli. Figure 6 shows the frequency of seeing curves and the fitted lines for each data set. The staircase procedure and the method of constant stimuli yielded very similar thresholds in this animal: 6.4' (staircase procedure) and 6.7' (constant stimuli;(Table 3a).

The four remaining cats were tested on the three stimulus sets with a single psychophysical procedure. Figure 7 shows their frequency of seeing curves. The estimated thresholds on all stimuli ranged from 2.2' to 6.1'. There are no threshold variations across stimulus sets (Table 3b).

After completion of testing on the three stimulus sets, one cat (MK80) was retested on grating 1 at the original viewing distance (50cm) and at 75 cm. This animal's threshold was 3.4' at the original viewing distance and 3.6' at 75 cm. These two values are very similar to one another and to the cat's performance on the original testing with grating 1 (3.3').

FIGURE 6. Frequency of seeing curves and fitted lines for MK58 on Grating 1 using the staircase procedure (top) and the method of constant stimuli (bottom).

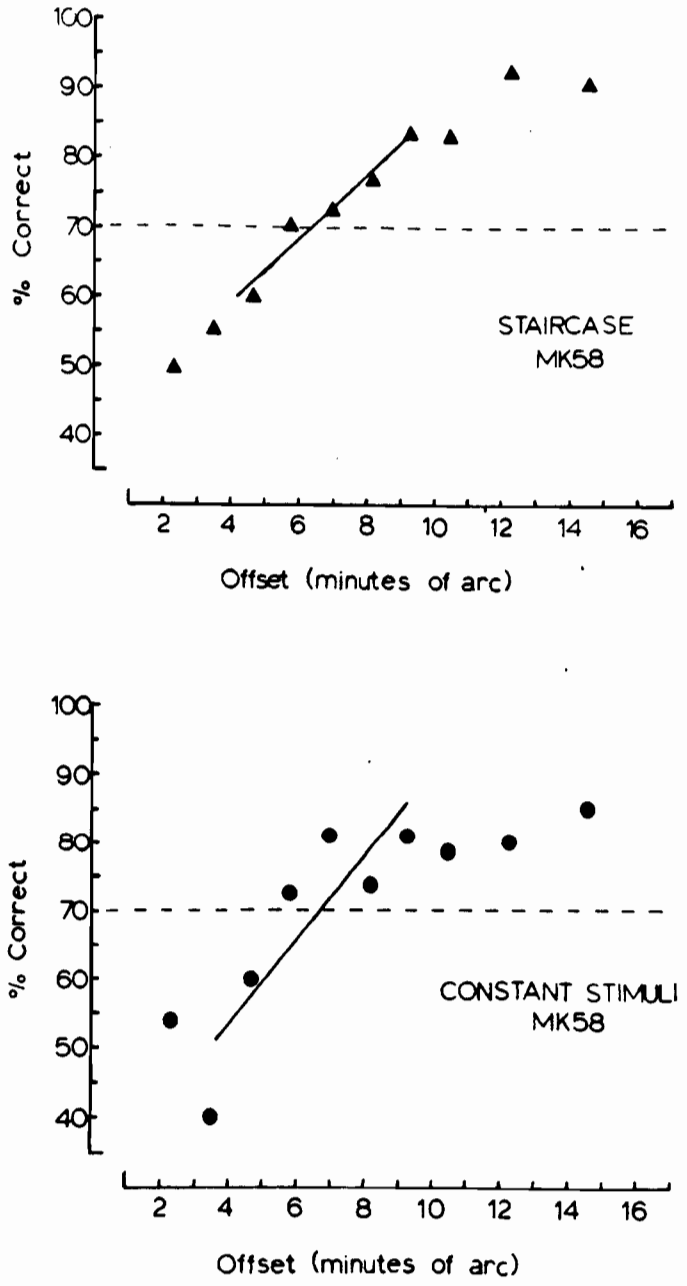
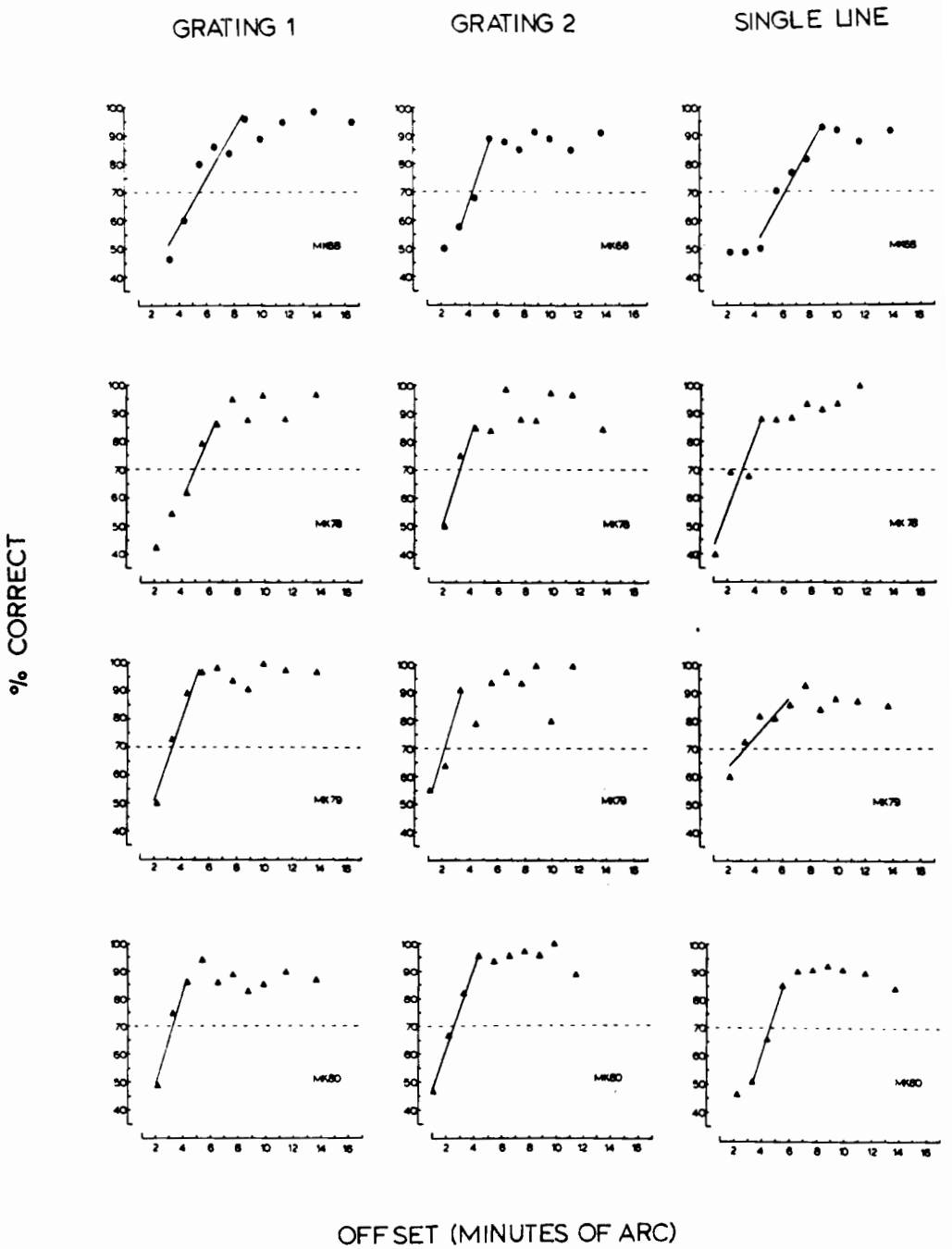


FIGURE 7. Frequency of seeing curves and fitted lines for four animals tested on Grating 1, Grating 2, and on the single line.



Discussion

The vernier task is difficult for cats to learn and they require a large number of trials to reach criterion. One of the reasons may be that the relevant information (the vernier offset) is located in a limited portion of the stimulus. However, when the cats learn the task they maintain a high level of performance on the large offsets. As offset size is decreased their performance rapidly falls to chance level on small offsets. Vernier thresholds were found to range from 2.2' to 6.7' with most values around 3' of arc. The observed range of threshold values can not be explained in terms of procedure (staircase vs constant stimuli) because, when used in the same cat (MK58), the two psychophysical methods yielded very similar thresholds: 6.7' and 6.4' (see Table 3a).

The importance of practice in vernier performance has been emphasized in the human literature (Westheimer and Hauske, 1975). For this reason, it is important to note that the threshold values were determined following extensive over-training on various offset sizes (520-3040 trials). It is also worth noting that the measured thresholds of the cats with the smallest number of practice trials (5' and 3.3' in MK78 and MK79) are comparable to those of other cats, as is the performance of the cat with the largest number of trials (5.4' in MK68). Furthermore, no significant improvement was found as a function of presentation order. Such an effect would have been expected if the cats had

not performed at an optimal level on the first stimulus set. Hence, the thresholds reported here are probably representative of the best performance these cats could achieve under those particular testing conditions. The data of MK80 further supports this conclusion. This cat was retested on Grating 1 at two different heights at completion of testing on the three stimulus sets. At both viewing distances, this animal showed a threshold performance almost identical to its first performance on Grating 1 (3.4 and 3.6' vs. 3.3').

This extensive examination of vernier acuity in normal cats was undertaken to see if thresholds in the hyperacuity range could be obtained using a more salient stimulus than the short single line target used in earlier work (Berkley and Bush, 1983; Berkley and Sprague, 1979; Sprague et al., 1979). The thresholds reported by these investigators (4-8') overlap the upper end of our range. The present thresholds were about twice as good as those reported by Berkley and Sprague, even though a more conservative threshold estimate was used (70% in the present study, 56% in Berkley and Sprague's study). If a less conservative threshold criterion (60%) is applied to our cats' performance, thresholds range from 1.4' to 5' (Table 3). Our cats did not perform significantly better on the grating stimuli than on the single line which indicates that under our testing conditions, the single line is as effective a target as the grating stimuli. Consequently, it appears that some factors which remained constant across the present testing conditions

contributed to better vernier detection than reported in previous studies.

A number of factors may explain the better offset detection in the present testing situation. Although threshold differences were not found between grating and single line stimuli, it is possible that all our stimuli were more salient because they cover a larger surface area than the 5^{o} line segment of the previous study. It should also be noted that the luminance level was about 1 log unit lower in the previous study than in ours, although it was in the photopic range. Luminance level may play a role in offset detection but it is doubtful that it is the critical factor because our estimates of resolution acuity made under similar lighting conditions are not better (see chapter 7) than the ones reported by Berkley and Sprague (1979).

CHAPTER 4

EXPERIMENT 2

STRIATE CORTEX INVOLVEMENT IN VERNIER ACUITY

All visual information that passes from the eye to the brain is transmitted along the axons of the ganglion cells, the properties of which have been extensively documented. Independent of the classical center-surround type of classification (Kuffler, 1953), three functional classes of ganglion cells have been identified in the cat visual system (X-, Y-, and W- cells or brisk-sustained, brisk-transient, and sluggish, respectively), according to their physiological properties (Cleland and Levick, 1974; Cleland, Harding and Tulunay-Keesey, 1979; Enroth-Cugell and Robson, 1966; Ikeda and Wright, 1972). The X-cells show high spatial resolution and have smaller receptive fields than the Y-cells. Electrophysiologically classified cell types have been correlated with morphological classes of cells (Fukuda, Hsio, Watanabe and Ito, 1984). Alpha cells have a large cell body (about 30μm), a large dendritic field and correspond to Y-cells (Boycott and Wassle, 1974; Fukuda et al., 1984). Beta cells have a medium-size cell body, a small bushy dendritic field and correspond to X-cells (Boycott and Wassle, 1974; Fukuda et al., 1984).

Area 17 is the exclusive projection site of X-cells though it also receives Y- and W- afferents. Area 18 receives a large

projection from the Y-cells but also receives W-cells input. Area 19 receives a major W-cell input but also receives Y-cell projections (Burrows and Hayhow, 1971; Cleland, Dubin and Levick, 1971; Geisert, 1980, 1985; Levay and Gilbert, 1976; Hollander and Vanegas, 1977; Kratz, Webb and Sherman, 1978; Maciewicz, 1975; Razkowski and Rosenquist, 1980). Their physiological properties as well as their projection pattern lead to the suggestion that X and Y functional classes of cells are involved in different types of visual processing. One hypothesis suggests that X-cells are involved in fine visual analysis (spatial vision) and Y-cells in movement detection (temporal vision; Stone, 1983). An alternative view proposes that both types are involved in spatial vision by filtering either the high (X-cells) or the low (Y-cells) spatial frequency content of the stimuli. The Y-cells would provide a coarse analysis that would temporally precede a fine-grained analysis provided by X-cells (Cleland et al., 1979; Sestokas and Lemkuhle, 1986). In any case, it is clear that X-cells are responsible for the visual analysis of fine high spatial frequency stimuli and are relevant to the understanding of vernier acuity.

Area 17 is a well-ordered topological representation of the visual field with a disproportionate amount of tissue devoted to the area centralis (Tusa, Palmer and Rosenquist, 1978). Units in area 17 have elongated receptive fields tuned to orientation and direction (Bishop, Kato and Orban, 1980; Hubel and Wiesel, 1962; Leventhal and Hirsch, 1978). Both monocular and binocular units have been found in area 17 (Hubel and Wiesel, 1962). The

preferred spatial frequency of units (simple cells with a receptive field within the central 5^{o}) in area 17 range between 0.3 to 3 cycles per degree (Movshon, Thompson and Tolhurst, 1978).

The characteristics of area 17 - fine-grained map of the visual field, cells tightly tuned for orientation, only recipient of the X-cell projection system - strongly suggest that this area is involved in fine analysis of the visual scene. Its removal should therefore preclude behavioural tasks that require precise positional analysis such as vernier acuity.

In cats, removal of the visual cortex results in severe atrophy of the LGN and degeneration in the medial interlaminar nucleus (MIN) (Wood, Spear and Braun, 1974). Behaviourally, removal of areas 17-18-19 results in a loss of pre-operatively learned simple (Cornwell and Warren, 1981; Cornwell, Overman and Campbell, 1980; Doty, 1961; Murphy, Mize and Schechter, 1975; Winans, 1971) or complex pattern discrimination (Tucker, Kling and Scharlock, 1968; Cornwell et al., 1980). These cats are however capable of recovering rudimentary vision with extensive training (Spear, 1979; Spear and Braun, 1969; Wood et al., 1974) and this recovery has been attributed to the posteromedial lateral suprasylvian (LS) cortex (Spear and Baumann, 1979).

Following smaller lesions restricted to areas 17 and 18, laminae A and A1 undergo complete atrophy and lamina C shows a marked but not complete degeneration (Sprague, Levy, DiBardino and Berlucchi, 1977). Laminae C1 and C2 are left intact and MIN is relatively preserved (Sprague et al., 1977). This is

accompanied by immediate changes in the response properties of the LS neurons (Spear and Bauman, 1979). Cells in LS are known to be sensitive to moving objects, direction selective and binocularly driven. Following ablation of area 17 and 18, the percentage of cells that respond to stationary flashing stimuli increases markedly. Moreover, there is a marked reduction in the percentage of direction selective cells (from 80% to about 20%), and a loss of response to the ipsilateral eye (Spear and Bauman, 1979).

The learning of form and pattern discrimination is only slowed down after areas 17-18 lesions (Cornwell and Warren, 1981; Spear and Braun, 1969; Sprague et al., 1977). However, area 17-18 lesions were found to produce impairments in discriminating forms behind visual masking (Cornwell et al., 1980; Hoffman and Von Seelen, 1984), in tasks that require local analysis (Hughes, 1982; Sprague, Hughes and Berlucchi, 1981) and in finely tuned tasks (Berkley and Sprague, 1979; Berkley and Bush, 1983; Kaye, Mitchell and Cynader, 1981). Even though resolution acuity is only about 20% worse after removal of areas 17-18, orientation acuity is dramatically impaired (3 times worse; Berkley and Bush, 1983; Berkley and Sprague, 1979; Sprague et al., 1979) and stereopsis is eliminated (Kaye et al., 1981).

Striate cortex was implicated in vernier acuity, in a study which measured vernier acuity in three lesioned cats (Berkley and Sprague, 1979; Sprague et al., 1979). Only one cat was tested both pre- and post-operatively. This animal had a threshold of about 6' pre-operatively and could not relearn the task

post-operatively. The other two cats were tested post-operatively only; one exhibited a 60' threshold and the other never learned the task. There are, however, a number of difficulties in interpreting the data of this study. Threshold measurement is a quantification of the sensitivity of a system and refers to the limit of an ability. In the case of vernier acuity, it is the smallest misalignment offset that can be perceived. It is therefore mandatory to measure performance on a number of offset sizes in order to infer the acuity threshold of an animal. In that study, nothing is known about the actual acuity in two of the lesioned animals because they did not learn the task post-operatively. Since Berkley's paradigm was suggested to lack the salience necessary to elicit optimal performance from normal animals (see Chapter 3), it is possible that the severe deficits reported by these investigators in lesioned cats may be partly accounted for by these same factors.

This part of the study was conducted in an attempt to elucidate the role of striate cortex in vernier acuity using pre- and post-operative measurements made under conditions that should maximize the salience of the task. The confirmation of vernier deficits after a lesion restricted to the central representation of area 17 and 18 would shed light on the essential role of striate cortex in this ability. The justification of the lesion site is both anatomical and historical. Classically, areas 17 and 18 of cat visual system have been considered a functional unit. This is because lesions of 17 alone or 17 with 18 cause a similar degeneration pattern in LGN and because they both seem to be

involved in the same type of visual analysis (Sprague et al., 1977). Anatomically, the main justification arises from the fact that both areas share the representation of the vertical meridian and that removal of area centralis in area 17 can not be done without that in area 18.

Two cats (MK86, MK88) sustained removal of the portion of areas 17 and 18 that represents the central visual field (Tusa et al, 1978, 1979) in adulthood (after 6 months of age). The lesion was restricted to the part of area 17-18 that represents the area centralis because vernier acuity is a fine ability that depends essentially on the spatial precision of central vision and decreases dramatically with eccentricity. In addition, by restricting the lesion to this portion of the striate cortex other cortical areas were left intact.

Method

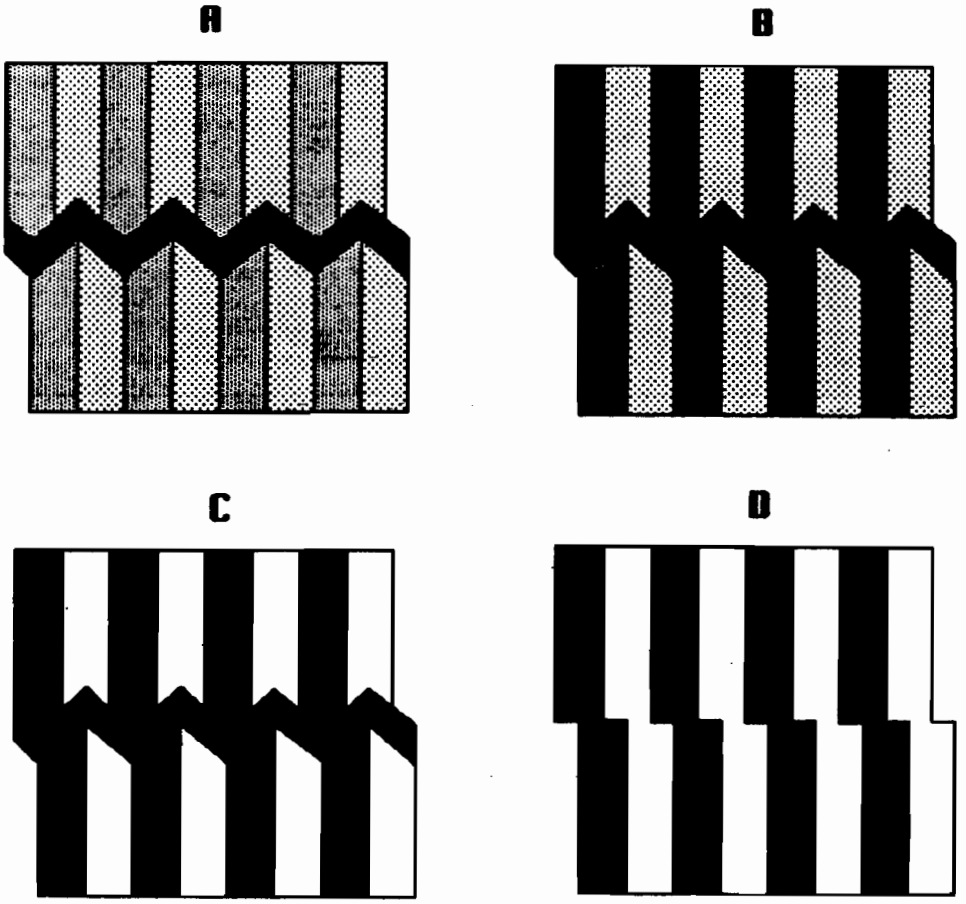
Procedure

Vernier thresholds were measured both pre-operatively and post-operatively using Grating 1 as the stimulus target. Before surgery, these animals were used as subjects in a developmental study of vernier acuity which is described later in this thesis. Briefly, their pre-operative training and testing extended over a period of 4 months. In general, testing conditions were similar to those described in chapters 2 and 3 with some minor differences which are explained in Chapter 5. Pre-operative

thresholds were the final values reached at 100 days of age using a staircase procedure similar in most details to that described in Experiment 1. After completion of threshold estimation and before surgery, animals were given practice trials on various offset sizes in order to maintain their performance level.

Post-operatively, cats were retrained using a fading-in technique. The goal of the technique is to attract the attention of cats toward the portion of the positive stimulus where the offset is located (the middle portion). The stimuli used in the fading-in technique are schematically presented in Figure 8. A wide (1.2 cm) jagged line was superimposed on a very low contrast grating. The positive stimulus was the grating with the jagged line while the negative stimulus was the same grating with no jagged line (or offset). After reaching criterion (27/30 correct response) the contrast of the background grating was gradually increased to a high contrast grating (A to C in Figure 8; 2 steps: 9/10 correct criterion for each step). The jagged line was then replaced by a large offset (1.1^{o} at 40 cm; D on Figure 8). Following criterion on this last transfer task, cats were transferred to Grating 1. The cats were given practice trials (240 for MK88 and 300 for MK86) and thresholds were measured again with Grating 1 and the staircase procedure (Staircase 2) used pre-operatively. This staircase procedure differed from the one used in the previous chapter in the number

FIGURE 8. Schematic diagram of the stimuli used in the fading-in technique. A: Low contrast grating with jagged line. B: Medium contrast grating with jagged line. C: High contrast grating with the jagged line. D: High contrast grating.



of trials given at each offset size. As will be seen in Chapter 5, this staircase procedure yields thresholds in normal adult cats that are comparable to the threshold values previously reported in Chapter 3. However, in order to ensure that the procedure did not cause a disadvantage to the lesioned animals, at the end of threshold measurement, they were retested using the staircase procedure (Staircase 1) described in Chapter 3.

Surgery

The adult lesions were done at the Department of Psychology of Université de Montréal by Dr. Franco Lepore. They were performed under complete aseptic conditions. Animals were anaesthetised with halothane. Atropine (1 cc) was given to avoid respiratory problems and dexamethasone was provided to prevent the brain from swelling. The head was held in a cat stereotaxic apparatus. The scalp was incised and retracted and a square piece of skull overlying the striate cortex was cut and removed. This piece of bone was temporarily placed in physiological saline. The dura and the pia were cut and gently retracted. The lesion was performed by aspiration and intended to include the portion of areas 17 and 18 that represents the central visual field based on the report of Tusa and collaborators (1978, 1979). After the lesion was completed, the pia was gently replaced. Absorbable hemostat was placed on top to replace the dura. The bone was replaced and the muscles and skin sutured. An antibiotic powder (Neosporin) was applied on the sutured muscles. A topical

antibacterial agent (furazolidone powder) was externally applied. Animals were kept in a warm place until they completely recovered from the anaethesia. Derapene (1 cc) was injected i.m. just after the surgery, once a day for the following four days and once a week for the next three weeks as a prophylactic.

Histology

At the completion of testing, animals were perfused through the heart under lethal doses of sodium pentobarbital with 0.9% saline followed by 10% formalin. The brains were stored in 10% formalin for at least 1-2 weeks. They were then placed in a 30% sucrose formalin solution until they sank, embedded in gelatin-albumin following the procedure of Crane and Goldman (1979) and replaced in sucrose formalin for about 4 days. Frozen sections were cut at 30 μm thickness, keeping for histological preparation every second section at the level of the LGN, every fourth section at the level of MIN and lateralis-posterior pulvinar complex (or pulvinar) and every tenth section in the other parts of the brain. Of the sections retained, every fourth was stained with the Kluver-Barrera (1953) fiber stain technique and the remaining, stained with Cresyl violet Nissl stain.

The extent of the cortical lesion was assessed for each animal by examining the stained sections. The lesions were reconstructed by plotting their cortical extent in 1 mm steps on surface maps adapted from the atlas of Reinoso-Suarez (1961). Verification in terms of visual field representation was made using Tusa's electrophysiological work (Tusa and Palmer, 1980;

Tusa et al., 1978, 1979). In addition, a detailed analysis was made of the extent and pattern of retrograde degeneration in the LGN, MIN and pulvinar using coronal sections plotted at 240 μm intervals. The interpretation of the pattern of retrograde degeneration in relation to cortical areas damaged was based on published reports (Burrows and Hayhow, 1971; LeVay and Gilbert, 1976; Raczkowski and Rosenquist, 1980). Degeneration in the LGN was also compared to the visuotopic map of Sanderson (1971).

Results

Histological Results

The extent of the lesions was determined by analysing the cortical borders and pattern of degeneration in LGN, MIN and pulvinar. The cortical extent of the lesion as well as the pattern of degeneration in the LGN are shown on Figure 9 for MK86 and Figure 10 for MK88. In both cats, lesions were small and included only the parts of area 17 and 18 which represent the area centralis. The thalamic sections showed healthy cells in MIN and pulvinar. In the LGN, degeneration was consistent with the cortical extent of the lesion. No degeneration was found in lamina C. On coronal sections, degeneration was apparent in the antero-medial part of the laminae A and A1 in both sides. Degenerated areas were characterised by small shrunken cells and an abnormally high proportion of glia cells. In MK86 the removal

FIGURE 9. Diagram of the lesion extent in MK86. Coronal sections through the cortex (numbers indicate the level on the sagital plane) and pattern of retrograde degeneration in the LGN. Lesioned tissue and degeneration is indicated in black. The Figure also shows a surface view of the lesion extent (dotted area).

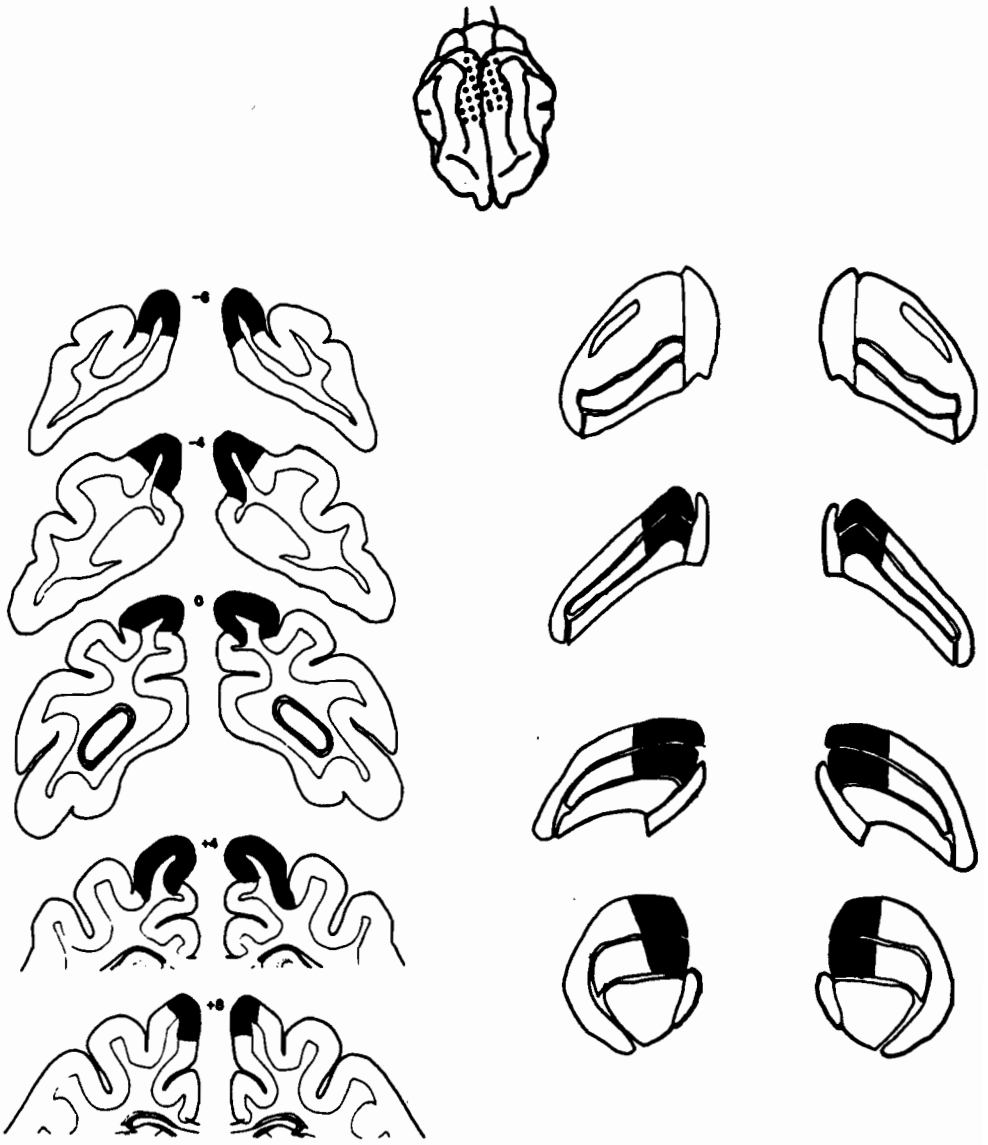
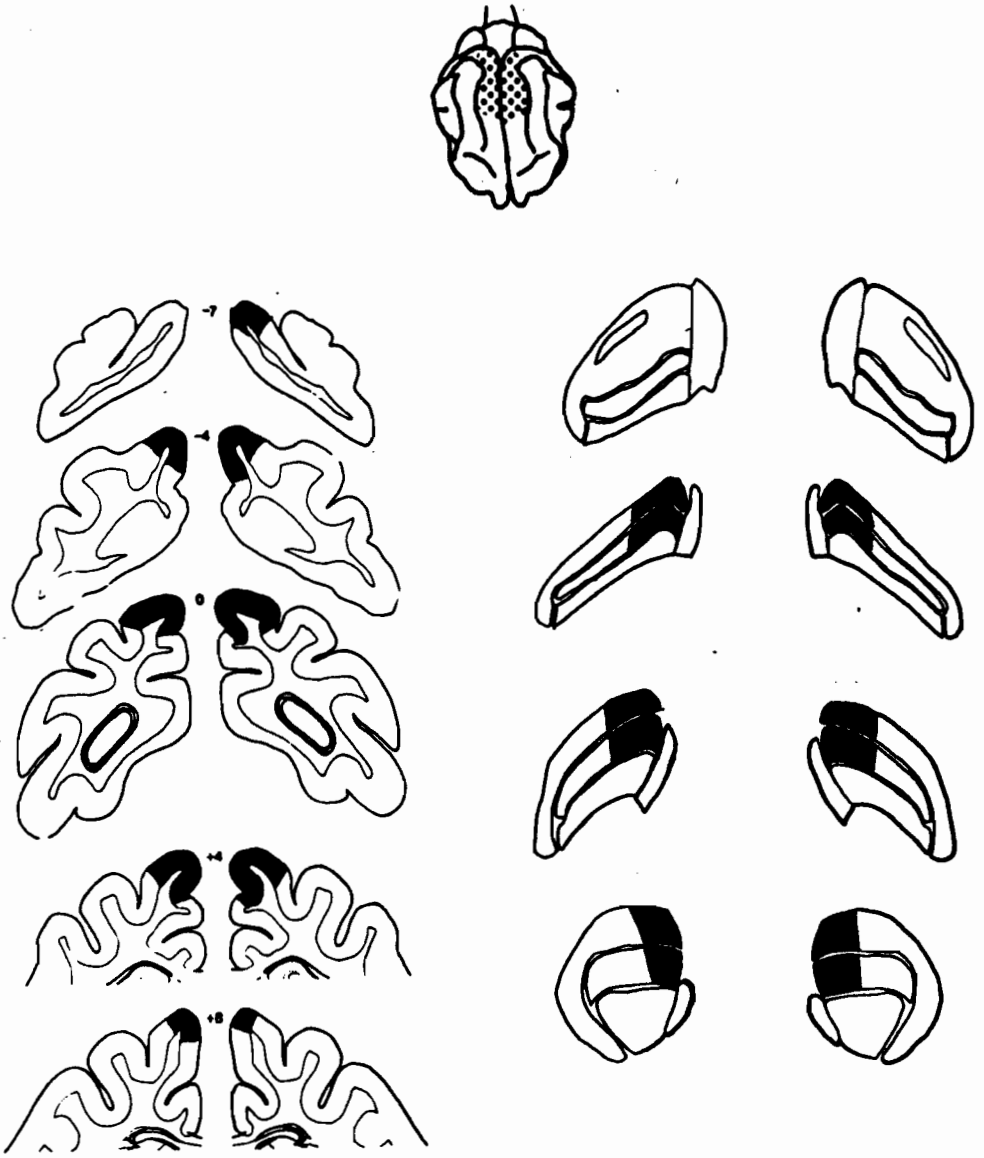


FIGURE 10. Diagram of the lesion extent in MK88. Coronal sections through the cortex (numbers indicate the level on the sagital plane) and pattern of retrograde degeneration in the LGN. Lesioned tissue and degeneration is indicated in black. The Figure also shows a surface view of the lesion extent (dotted area).



was very similar in each hemisphere. It included the representation of the central visual field in 17-18 up to about 10° eccentricity along the horizontal meridian, with narrowing above and below the zero meridian on both sides. Along the vertical meridian the lesion extends to 15° eccentricity in the lower visual field and 5° in the upper visual field. In MK88, the ablation was very similar and included the parts of areas 17-18 which represent the central visual field out to 5-8° eccentricity along the horizontal meridian. Very little damage was found in the field above the horizontal meridian as the lesion included up to about 3-5° eccentricity in the upper visual field, but it was more extensive, up to 10°, in the lower field.

Behavioural Results

In order to relearn the vernier task MK86 required 50 trials and MK88 108 trials (number of trials to transfer from the high contrast jagged line to the vernier stimulus). When they had learned the task, the cats performed well on large offset sizes but their performance dropped rapidly to chance values as offset size decreased. A frequency of seeing curve was derived from the performance of the cats on a large number of trials and the same procedure as described in Chapter 2 was used to obtain their vernier thresholds. Table 4 gives the pre-operative (Staircase 2: S2) and the post-operative (Staircase 2 and 1: S2 and S1) threshold values for the two cats. MK86's threshold was 1.6' of arc pre-operatively and 22.1' of arc post-operatively. Pre-operative and post-operative threshold values were 3.7' of

TABLE 4. This Table gives the pre-operative and post-operative thresholds for MK86 and MK88. S1: Staircase 1; S2: Staircase 2.

CAT	PRE-OPERATIVE THRESHOLD	POST-OPERATIVE THRESHOLD	
	S1	S2	S1
MK86	1.6'	22.1'	20.1'
MK88	3.7'	22.4'	21.8'

arc and 22.4' of arc, respectively, for MK88. The type of staircase procedure used did not affect the performance of the lesioned animals. The performance of both cats was almost identical using either procedure: 22.1' and 20.1' for MK86 and 22.4' and 21.8' for MK88 with the Staircase 2 and the Staircase 1, respectively (See Table 4).

Discussion

In the present study, in contrast to the findings of Berkley and Sprague, cats which had sustained a removal of the striate cortex relearned the vernier task easily. The fading-in technique used as the retraining procedure in the present study was probably a facilitatory factor for the relearning of the task.

Despite good learning performance, the post-operative thresholds of our lesioned animals were 6-13 times worse than pre-operative values. In Berkley and Sprague's study, the animal for which post-operative performance is available has a post-operative threshold of 1^{o} (60'). Since this subject was only tested post-operatively we can not compare its post-operative performance to a pre-operative level. However, if we compare it to other normal cats in their study, this post-operative threshold is about 12 times worse than normal performance. In terms of threshold, the post-operative performance of our lesioned cats is significantly better than that of Berkley's cat (17' as compared to 1^{o}). However, our cats' pre-operative

thresholds were also better than those reported in Berkley and Sprague's study. It is possible that our testing conditions (stimulus salience, luminance, testing procedure) which support better vernier performance in normal cats also partly account for the better performance of our lesioned animals.

These results clearly show that cats without striate cortex do not perform well in the vernier task. Even if the lesion is restricted to the portion of area 17-18 that represents area centralis, the performance level is much reduced as compared to their pre-operative abilities. However, this is not surprising given that vernier acuity is at its best in central vision and declines dramatically with eccentricity.

In terms of neural substrates, the striate cortex has a number of characteristics that makes it a likely candidate for vernier acuity processing. It is densely packed (especially layer IVCβ) and has a precise topographic representation of the visual field (Barlow, 1979, 1981; Crick et al., 1981). Furthermore, cells have been found in the cat striate cortex that respond to offset displacement smaller than their receptive fields (Swindale and Cynader, 1986). The present results further confirm the involvement of striate cortex in cat vernier acuity.

In spite of the observed increase in threshold, the cats retained the ability to perform the vernier detection task at large offsets post-operatively. The residual spatial analysis reflected in the post-operative threshold might have been performed by extra-striate mechanisms, possibly area 19. However, the lesions in these two cats were very small. Despite careful

examination of head position during testing, one could still argue that the cats were using spared peripheral tissue to perform the task. Therefore, we are not on firm ground to conclude that the observed thresholds reflect the capacity of an extra-striate substrate. Nevertheless, the evidence remains strong that striate cortex is essential for the precision of positional analysis displayed by normal cats.

CHAPTER 5

EXPERIMENT 3: THE DEVELOPMENT OF VERNIER ACUITY IN NORMAL CATS

Whereas the development of resolution acuity has been extensively studied both with behavioural techniques and evoked potentials (Birch et al., 1983; Dobson and Teller, 1978; Held, 1979; Mayer and Dobson, 1980, 1982, 1983; Norcia and Tyler, 1985; Sokol and Moskowitz, 1985; Van Hof-Van Duin, 1986), only recently has the development of vernier acuity been investigated in humans (Manny and Klein, 1985, Shimojo and Held, 1987; Shimojo et al., 1984). The development of vernier acuity is rapid during the early months of life and parallels that of stereoacuity, another hyperacuity (Birch et al., 1982, Birch et al., 1985, Shimojo et al, 1984), but differs from the development of resolution acuity (Shimojo et al., 1984).

In cats, resolution acuity develops gradually and reaches adult level around 110 days (Giffin and Mitchell, 1978; Mitchell et al. 1976) whereas stereoacuity is well developed by 90 days (Timney, 1981, 1983, 1984). The development of vernier acuity has not been studied in this species. The cat is a good model to study the development of vision because of the relative immaturity of its visual system at birth and because the development of its visual system is relatively well understood.

In addition, the cat is thus far the only animal model in which vernier acuity has been investigated physiologically at the single cell level (Shapley and Victor, 1986; Swindale and Cynader, 1986). The present study was undertaken to shed light on the course of vernier development in a species other than human and to compare it to human vernier acuity development.

Method

Subjects

Vernier acuity was measured in nine kittens. Kittens were kept with their littermates and mother until weaning. Afterward they were housed in pairs until about 2 months of age and then, individually. Kittens received food and water ad libitum. In addition to the daily portion of dry food (Purina cat chow), the nursing mother and kittens received a daily portion of wet food (Romar). A weaning formula (Borden kitten weaning formula) was also provided to very young kittens after separation from the mother. At testing onset the animals were 33 to 51 days of age (Table 5). Their daily thresholds were first measured between day 46 and day 67 (Table 5).

Procedure

As demonstrated in Experiment 1, the vernier task is difficult for cats to learn even as adults. Therefore, we used

TABLE 5. Age at onset of testing, age at beginning of threshold measurement and age at asymptote for the nine kittens.

CAT	AGE AT ONSET OF TESTING (DAYS)	AGE AT BEGINNING OF THRESHOLD MEASUREMENT (DAYS)	AGE AT ASYMPTOTE (DAYS)
MK83	47	66	70
MK85	47	67	76
MK86	47	58	71
MK87	41	49	78
MK88	41	51	74
MK89	41	60	83
MK93	51	62	87
MK94	51	55	90
MK96	33	46	83

the fading-in procedure (see Chapter 4) for infants. The purpose of this procedure is to minimize the number of trials required to reach criterion on the discrimination task. This is particularly important in a developmental study where one goal is to measure thresholds as early as possible. Following criterion performance on the last transfer task of the fading-in technique (see Chapter 4), kittens were transferred to Grating 1 and given a day of practice using the staircase procedure. Thresholds were then measured daily with Grating 1.

Psychophysical Procedure

In the developmental study, thresholds were determined daily and, in order to optimize the number of trials at near threshold offset sizes, the following modifications were applied to the staircase procedure described in Chapter 2. Stimuli were presented in decreasing order of offset size. The larger offsets were presented in blocks of two trials. If the kitten succeeded on both trials, the next offset size in the series was presented. Offsets around threshold (estimated from the threshold performance on the preceding day) were presented in blocks of five trials. If the cat scored 4/5 or better, the next smallest offset was presented. Failure (3/5 or worse) on any of the stimuli produced a three step increase in the offset series (See Appendix 1). The procedure was continued over 40 trials in a single daily testing session. There were enough trials in one session to complete at least two or three threshold runs. It

should be noted that the last run of a session was always continued until a failure occured. Consequently, more than 40 trials were sometimes required to complete one testing session.

The kittens' tolerance to the procedure was generally good. However, certain training rules were applied when they did not react appropriately to the testing situation. At beginning of testing (when kittens were very young) food was given warm to ensure eating. If they did not look at the stimulus or appeared distracted by irrelevant aspects of the testing room, noise was produced on the doors that bore the stimuli in order to attract their attention. When they refused to jump, they were gently pushed, but if they showed any sign of distress they were taken back through the initial steps of training.

Daily thresholds were measured until thresholds reached a stable level and continued for about 20 days. The asymptotic value was determined from the average performance on the last four days of testing (within two standard deviations variation). In one case (MK96) testing was continued for more than 60 days (until day 151) to ensure that no further improvement would occur. Furthermore, after completion of testing at asymptote, MK86 was retested at a greater viewing distance (75 cm).

Results

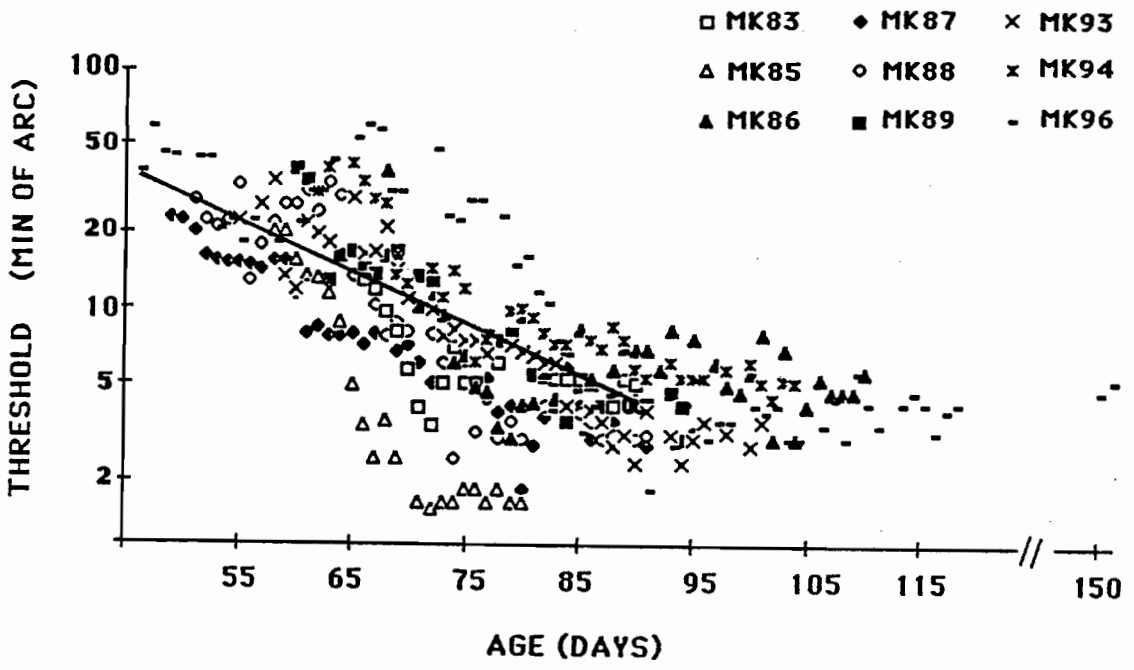
Table 6 shows the number of trials to criterion for all kittens on each step of the training sequence. There is considerable inter-individual variation: whereas some kittens went through the sequence very quickly (MK93: 76 trials excluding criterion trials) others took much longer (MK89: 732 trials excluding criterion trials). These inter-individual differences in the number of trials to criterion were not due to age at which testing was started since no correlation exists between age at beginning of testing and trials to criterion ($r=0.08$, $p>0.05$). Once kittens had learned the first task in the fading-in series they usually transferred quite easily to the remaining stimuli (see Table 6).

The daily performance of each animal was plotted against offset size on a linear scale. Daily thresholds were determined from the resulting frequency of seeing curve by joining the points and interpolating the vernier offset that corresponded to the 70% correct performance. Figure 11 illustrates the developmental function of vernier thresholds in the nine subjects. All but two cats reached asymptote (2-6') before 85 days of age. One cat reached as small a threshold as 1.5' of arc at 71 days of age. The measured threshold improvement does not reflect merely a practice effect because the ages at beginnning of both testing and threshold measurement do not correlate

TABLE 6. Learning trials (excluding the criterion trials) on the Fading-in technique for the nine normal kittens of Experiment 3. The sign (-) indicates immediate transfer.

CAT	GRATING A	GRATING B	GRATING C	GRATING 1
MK83	317	143	4	25
MK85	530	4	8	7
MK86	154	-	-	1
MK87	187	29	23	15
MK88	297	7	16	3
MK89	657	-	50	25
MK93	73	-	-	3
MK94	371	10	10	30
MK96	4	40	10	202

FIGURE 11. Developmental function in the normal kittens. Each sign represents a different animal. One cat was tested until day 151. The performance of that cat on the last two days of testing is shown. The fitted line is also shown on this Figure.



positively with the ages at which kittens reached asympotic performance ($r=0.11$, $p>0.05$ and $r=-0.24$, $p>0.05$, respectively). A line was fitted to the natural log thresholds with linear regression analysis. For each subject, we included in the analysis all the daily thresholds until the asympotic level was reached (the first day of the asymptote was included). The analysis yielded the following model for the developmental data: $Logx= -0.05y + 5.8$ ($r^2=0.42$, $F=233.16$, $p<0.01$). The model has a high significance level and a good correlation value which indicate that the log linear function was appropriate to fit the data. According to the model, vernier acuity is about 33' at 46 days.

Animals were tested for many days after they reached asymptotic values. One of them (MK96) was tested extensively until 151 days of age. No threshold improvement occured after 83 days of age (see Figure 11), which confirms that under our testing conditions vernier acuity is fully developed by 70-85 days of age. When retested at a larger viewing distance (75 cm), the threshold of MK86 was very similar to its first estimation from a 50 cm viewing distance (1.5' and 1.6' from a 50 cm and 75 cm viewing distance, respectively). This suggests that the estimation of the viewing distance in the first measurement was quite accurate.

Testing of each animal was continued until asymptotic performance. The data obtained at asymptote were treated in the same fashion as in Chapter 3 to obtain threshold estimates.

A frequency of seeing curve was determined individually for each cat from its performance on a large number of trials on each offset size. A line was fitted to the descending portion of the curve with regression analysis (see Chapter 3). The thresholds were determined by taking the offset size that corresponded to the 70% cutoff performance from the fitted line. The estimated thresholds (70%) ranged from 1.5' to 5.4' (Table 7). If we used a somewhat less conservative threshold criterion (60%), the estimated thresholds ranged from 1.3 to 4.5' (Table 7). The performance achieved by the cats at asymptote is very close to the performance of adult cats as shown in Experiment 1. Thus, it is unlikely that further improvement would have been measured if testing had continued to sexual maturity.

Discussion

Vernier acuity develops rapidly from initial values of about 33' of arc at 46 days of age to asymptotic values of 2-6' of arc at 71-90 days of age. The measured development was not found to be merely a practice effect because the day at which measurement was started did not correlate with the day at asymptote. In addition, extensive training (until 151 days) in one cat did not yield any threshold improvement (Figure 11). These are strong arguments that the data is a true reflection of the developmental pattern of vernier acuity.

TABLE 7. Adult vernier acuity thresholds (70% cutoff criterion) and 60% cutoff performance for the nine cats of Experiment 3.

CAT	VERNIER ACUITY THRESHOLD (70% CUTOFF)	60% CUTOFF PERFORMANCE
MK83	5.4'	4.1'
MK85	4.6'	3.6'
MK86	1.5'	1.3'
MK87	3.5'	2.1'
MK88	3.8'	2.7'
MK89	4.4'	3.5'
MK93	3.1'	2.5'
MK94	5.2'	4.5'
MK96	4.0'	2.8'

The vernier thresholds measured as adults range from 1.5 to 5.4' of arc. These thresholds are comparable to the values found in another group of normal adult cats using a somewhat different staircase procedure and constant stimuli (Chapter 3). This is important because it confirms the point made in Chapter 3 that thresholds are independent of the psychophysical procedure.

The developmental pattern of vernier acuity may be linked to several factors. Peripherally, some factors can be ruled out. The optical quality is well developed at 35 days (Bonds and freeman, 1978; Thorn et al., 1976). Refractive error can not be completely ruled out since cats are hypermetropic in the first 8 weeks of life (Flynn, Hamasaki, Flynn and Barrick, 1975). Photoreceptors are adult-like by about 30 days (Vogel, 1978). However, the developmental course of intercone spacing is not well documented and may be relevant to the development of vernier acuity. Interconnections in the inner plexiform layer develop slowly between 50 and 110 days (Hamasaki and Maguire, 1985; Vogel, 1978). If vernier acuity depends on the pooling of information over relatively wide retinal areas (Barlow, 1979; Westheimer, 1979; Westheimer and McKee, 1977a), its development may be related to the development of these interconnections. Interestingly, the electroretinogram components related specifically to cone-ganglion cell connections (cone bipolar cells) are fully developed by 80 days (Hamasaki and Maguire, 1985), the age at which asymptotic vernier acuity is reached.

Note also that whereas units have attained adult-like receptive field center physiological properties by about 3 weeks of age, the surround (its size and the strength of its inhibition) remains immature until 7 weeks (in peripheral units at least; Hamasaki and Flynn, 1977; Rusoff and Dubin, 1977).

Shimojo and Held (1987) recently suggested that, whereas the development of resolution acuity may be related to changes in the size of the receptive fields, the development of vernier acuity may be related to changes in their density. On the other hand, recent reports which indicate that cells at various levels in the visual system respond differentially to offsets smaller than their spatial resolution are suggestive of neuronal hyperacuity (Swindale and Cynader, 1986; Victor and Shapley, 1986). If these cells are involved in hyperacuity processing, the development of their sensitivity should parallel that of vernier acuity in cats.

CHAPTER 6

EXPERIMENT 4: THE EFFECT OF NEONATAL REMOVAL OF VISUAL CORTEX ON THE DEVELOPMENT OF VERNIER ACUITY

A number of studies examining the visual performance of cats following neonatal lesions of visual cortex have suggested that there is considerable sparing of visual function after early lesions (Doty, 1961; Murphy, Mize and Schechter, 1975; Tucker, Kling and Scharlock, 1968; Wetzel, Thompson, Horel and Meyer, 1965). It has been suggested that this sparing of function may be related to functional reorganization that occurs within the remaining visual pathways (Spear, 1979, 1984; Spear, Kalil and Tong, 1980a; Tong, Kalil and Spear, 1984).

Cats that have sustained neonatal ablation of cortical areas 17, 18 and 19 learn as rapidly as normal cats a number of visual discrimination problems including form and pattern discrimination (Doty, 1961; Murphy et al., 1975). In addition, they exhibit normal behaviour in photic frequency and brightness discrimination tasks (Tucker et al., 1968). On the same tasks, cats sustaining lesions as adults are much more impaired (Murphy et al., 1975, Tucker et al., 1968).

Anatomically, neonatal visual cortex lesions produce a large amount of degeneration in the LGN. The appearance of the LGN is characterized by an absence of its usual laminar pattern and

by the presence of large darkly stained cells sparsely scattered throughout the nucleus (Doty, 1961; Murphy et al, 1975, Tucker et al., 1968). The degeneration in the LGN is accompanied by a massive transneuronal degeneration of retinal ganglion cells that results in a large decrease in ganglion cell sampling density (Kalil, 1980; Pearson, Labar, Payne, Cornwell and Aggarwal, 1981; Spear, Tong, Kalil and Callahan, 1980b). Physiologically, experiments show that in very early lesions (day 1) this decrease can be accounted for by a severe loss of X-ganglion cells while Y- and W-cells remain relatively intact (Tong et al., 1984). Anatomical data agreed with the preceding finding by showing in the retina a marked decrease in the number of medium-sized cells (beta cells, the anatomical correlate of X-cells), while small sized (W-cells) and large sized cells (Y-cells) remained unaffected (Kalil, 1980, Pearson et al., 1981). The surviving ganglion cells provide at least two anomalous afferents to the thalamus: the first is to the geniculate wing, and the second is an unorganized input to the large surviving cells of the LGN (Kalil, 1978; Labar, Berman and Murphy, 1981). These LGN cells are visually responsive, they have the typical center-surround receptive-field but a looser topological organization and larger receptive-fields than normal (Kalil and Murphy, 1979).

The LS cortex has been implicated in the behavioural recovery that follows infant lesions (Spear, 1984; Spear et al., 1980a; Tong et al., 1984). Changes in the LGN input to LS were

observed after neonatal visual cortex lesions (Tong et al., 1984). In normal cats, the only projection from LGN to LS is a sparse input from the C-laminae (Levay and Gilbert, 1976; Maciewicz, 1975; Rosenquist, Edwards and Palmer, 1974). After a day 1 lesion of the visual cortex, there is a marked increase of the C-laminae input to LS and a new projection from laminae A and A1 (Kalil and Murphy, 1979; Spear et al., 1980a; Tong et al. 1984).

A number of studies have investigated physiological recovery following neonatal removal of the visual cortex (Spear, 1984; Spear et al., 1980a; Tong et al., 1984). Note that all the following results are based on unilateral lesions. Recording of single units in LS was carried out in adult cats which had received a lesion of areas 17-18 or 17-18-19 within the first 30 hours of life. Recording of cells in LS show normal physiological response properties: they remain direction selective, their tuning is normal, and most cells are driven by both eyes (Spear et al., 1980a; Tong et al., 1984). Consequently, neurons in LS develop normal response characteristics despite their lack of input from the removed areas (Spear et al., 1980a). If the lesion occurs in adulthood, there is an increased response to stationary stimuli, a loss of direction selectivity and a loss of response to the ipsilateral eye (Spear and Baumann, 1979; Spear et al., 1980a; Tong et al. 1984). Lesions that occur at intervening ages produce mixed effects (Tong et al., 1984). When the lesion occurs at 182 days of age, the cell properties are comparable to those

after an adult lesion; if it occurs at 126 days of age, ocular dominance is normal but there is an increased response to stationary stimuli. If, however, the lesion is done at 84 days, both ocular dominance and direction selectivity are normal (Tong et al., 1984). There are no orientation selective cells in the normal LS cortex, or after an adult or neonatal (day 1) lesion. Orientation selective cells are recorded in LS following a lesion of the visual cortex that occurs between 14 and 56 days of age (Tong et al., 1984).

The physiological and anatomical changes that follow early cortical lesions have been proposed as substrates for the behavioural recovery associated with such lesions. Questions remain about the actual behavioural abilities that this compensation can subserve. Despite the previously described functional compensations, cells do not develop properties similar to those in the removed cortex: they have large receptive fields, a loose spatial representation and, except when the lesion occurs between 14 and 56 days, they are not orientation selective (Spear et al., 1980a; Tong et al., 1984). In fact, even if some of the functions normally processed by areas 17-18-19 can be taken over by cells in LS, the precise selectivity of the removed cells is not reached and a limit to the extent of recovery is expected. In very early lesions, the significant loss of X-cells and the relative intactness of the other cell types is most probably related to the extent and type of recovery. The determination of the extent of visual

capabilities following early lesions will clarify the significance of the changes observed at the neural level.

The aforementioned behavioural studies were concerned with simple form and pattern discrimination. In fact, deficits have been reported in the discrimination of complex forms (Cornwell, Overman, and Ross, 1978) and in the ability to segment on the basis of textural grouping (Wilkinson and McCormick, 1984).

There is very little infomation on the psychophysical capacities of cats with neonatal visual cortex damage. Spear (1984) mentions a preliminary report (Kaye and Mitchell, personal communication) which found normal resolution acuity thresholds in cats with neonatal visual cortex damage but a loss of stereopsis.

Most of the studies which have demonstrated behavioural sparing have focused on tasks which seem to depend more on extra-striate than striate visual areas (form and pattern discrimination) (Sprague et al., 1977). As was shown in Chapter 4 and by previous investigators (Berkley and Bush, 1983; Berkley and Sprague, 1979; Sprague et al., 1979), vernier acuity is specifically related to the striate cortex and its physiological substrate is likely to involve the striate target of geniculate X-cells. Given the physiological properties of LS units and the substantial loss of X-cells following neonatal lesions, it is improbable that the physiological reorganization would provide a basis for the normal development of vernier acuity. The objective of the present undertaking was to examine the effect of neonatal lesions on the development of vernier acuity in cats

and on their vernier thresholds as adults. The reason for using a developmental approach in studying the effects of early lesions is that it provides a more dynamic image of a particular ability as it develops over time. This permits comparison with normal behavioural development and devolpment of underlying neural substrate.

Method

Subjects and Procedure

Vernier acuity thresholds were measured in four animals with neonatal lesions (MK73, MK91, MK92, MK95) and in three littermates whose data was previously shown (MK93 and MK94 which are littermates for MK91 and MK92, and MK96 which is littermate for MK95).

One cat (MK73) was lesioned in infancy but only tested as an adult. This cat was the first lesioned animal studied and the fading-in training procedure previously described had not yet been developed. As earlier attempts using offsets in a grating as the training procedure had proved unsuccessful, a very large offset (47 mm) in a single line was used as the training stimulus with this cat. The advantage of using a single line is that it is possible to introduce a very large offset which might increase its salience and facilitate learning. This was particularly important since it was not known yet over what

range the offset thresholds of the lesioned animals would fall. When the animal reached criterion (27 correct responses out of 30) on this stimulus, the offset was gradually decreased. Because the initial offset size was very large, this step required a large number of trials on smaller offset sizes. This cat's vernier threshold was then measured with Staircase 1 (described in Chapter 2) and the single line series. After completion of testing on the single line series, the animal was transferred to Grating 1 and its threshold measured again.

In the remaining six cats, vernier acuity was measured both developmentally and in adulthood. For these six cats, the fading-in technique was used as the training procedure (See chapter 3) and thresholds were measured with Grating 1 and Staircase 2. The procedure and stimuli were the same as previously described in Chapter 5. Table 8 shows for each cat age at onset of testing, age at beginning of threshold measurement, and age at asymptote. In order to ensure that no further improvement would occur, a large number of trials were given to the lesioned animals after they had reached asymptote. Furthermore, two cats (one control: MK95, and one lesioned: MK96, were tested extensively until 151 days of age.

Surgery and Histology

The lesions were performed under aseptic conditions before eye opening, at day 1 (MK91), day 2 (MK73), day 4 (MK92) and day 8 (MK95). Animals were anaesthetized with halothane. The scalp

TABLE 8. Age at onset of testing, beginning of threshold measurement and asymptote for the three lesioned kittens (MK91, MK92, MK95) and their control littermates (MK93, MK94, and MK96). L: lesioned subject; C: control littermate.

CAT	AGE AT ONSET OF TESTING (DAYS)	AGE AT BEGINNING OF THRESHOLD MEASUREMENT (DAYS)	AGE AT ASYMPTOTE (DAYS)
MK91 (L)	51	59	61
MK92 (L)	51	62	66
MK93 (C)	51	62	87
MK94 (C)	51	55	90
MK95 (L)	33	47	73
MK96 (C)	33	46	83

was incised and retracted. A rectangular piece of skull overlying striate cortex was removed on each side leaving intact the skull on the midline. The two pieces of bone were temporarily removed and kept in sterile physiological saline. The dura was cut and retracted. Lesions were done by aspiration and intended to include the portion of area 17 and 18 that represent the central visual field based on the maps of Tusa et al (1978, 1979). During surgery, a saline solution was injected subcutaneously to reestablish the animal's fluid balance. After the lesion was completed, gelfoam was used to fill the internal cavity left by the lesion and the dura and the bone pieces were gently replaced. Derapene (0.1 cc) was injected i.m. just after the surgery and once a day for the following three days. During the recovery phase, animals were placed under a warm lamp to maintain normal body temperature. They were replaced with their mother when they appeared strong enough to nurse (usually 1 to 2 hours post-operative). At completion of testing, animals were perfused and histological analysis carried out as described in Chapter 4.

Results

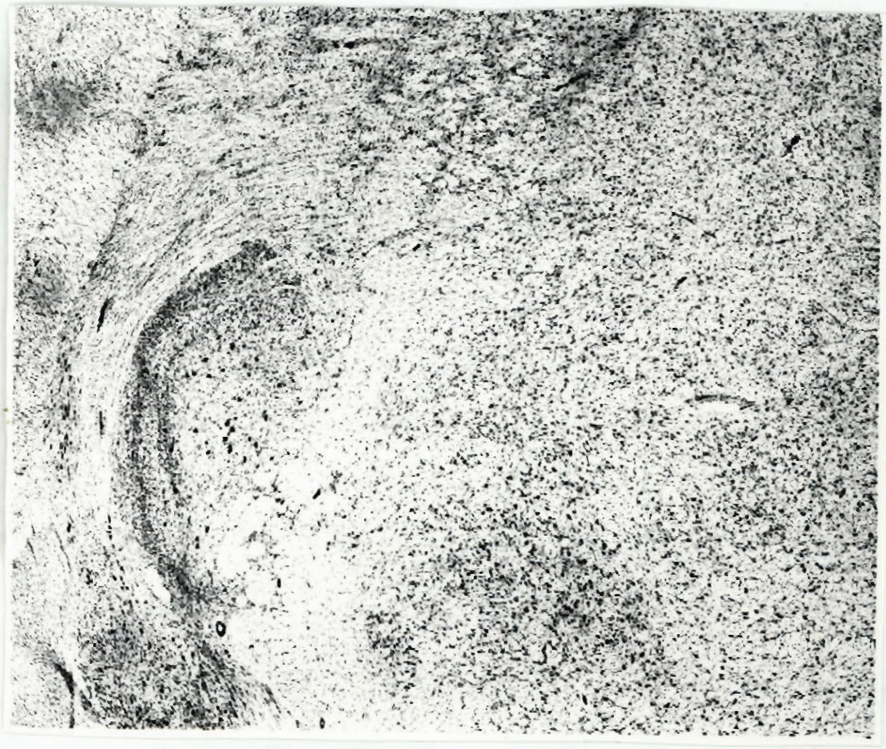
Histological Results

Analysis of the extent of the cortical lesions was based on a reconstruction of the cortical borders and on the analysis of the pattern and extent of retrograde degeneration in LGN and MIN as described in Chapter 4 and in the LP-pulvinar complex. The investigated sections showed a number of characteristics typical of early lesioned brains. (1) After an early lesion, the remaining cortical tissue is usually distorted in the internal cavity making the histological investigation of the cortical borders more difficult than after adult lesions. (2) In normal kittens, the LGN undergoes a rotation of its main axis during development from a ventro-dorsal to a rostro-caudal orientation (Henderson, 1982; Kalil, 1978). This rotation is, however, interrupted by an early lesion of visual cortex and as a result the main axis has a ventro-dorsal position. This was observed, though not to the same extent, in all of the lesioned animals. The visuotopic reconstruction of the LGN is not as straightforward in the neonatally as in the adult lesioned animals because of this immature position. To facilitate this work, three-dimensional models of the cortical lesion and of the LGN and MIN were completed in the four lesioned cats. However, for clarity,the present data are shown rotated onto standardized adult maps. (3) A number of investigators (Murphy et al., 1975;

Spear et al., 1980; Tucker et al., 1968) have reported the presence of large darkly stained cells sparsely scattered throughout the degenerated LGN after an early lesion. These cells do not correspond to spared tissue because they were also found in those parts of the nucleus that correspond to a totally removed cortex. Such cells were encountered in the brain sections from some of the neonatally lesioned cats in the present study. (4) Lastly, following a neonatal removal of the visual cortex, the LGN is characterized by very dense retrograde degeneration and disappearance of the laminar structure typical of the nucleus; this was also observed in the present study.

The analysis of cortical lesion extent was based on the electrophysiological work of Tusa and his collaborators (Tusa and Palmer, 1980; Tusa et al., 1978, 1979). The pattern of retrograde degeneration in the thalamic nuclei was interpreted according to previous findings (Garey and Powell, 1967; Niimi and Sprague, 1970; Sprague et al., 1977). Retrograde atrophy after areas 17-18 lesion is restricted to layers A and A1 while involvment of area 19 results in an additional marked atrophy of the deep layers and MIN. The visual field correspondence of LGN degeneration was based on Sanderson's work (1971). In the LGN, the vertical meridian is represented medially while the contralateral peripheral visual field is represented laterally. The lower visual field is represented anteriorly and the upper visual field posteriorly. Figure 12 shows an example of the

FIGURE 12. Photographic reprint which illustrates the severe atrophy in the LGN that follows a large cortical removal. (Magnification 12x).



severe atrophy that results from a large cortical neonatal removal (areas 17-18-19 in MK73). Finally, degeneration in the pulvinar results from lesions in the suprasylvian gyri and its analysis was based on the work of Hughes (1980) and on previous findings (Berlucchi, Sprague, Antonini and Simoni, 1979).

In all cats, there is close correspondence between the extent of cortical damage and the areas of severe degeneration in the thalamic nuclei. The lesions in these four early lesioned cats are more extensive than the ones presented in Chapter 4 (adult lesions). In two cats (MK73, MK92), the lesions were quite large and included most of 17, 18 and some part of area 19. The other two cats (MK91, MK95) had a smaller lesion that included the central portion of area 17-18. A summary of the histological analysis follows. For each cat, the description of the removal extent is illustrated by a figure which shows a surface view of the brain and coronal sections through the cortical lesions, LGN and MIN. The level of the LGN is not indicated since, as was previously explained, these are rotated representations. Note that in these figures, the cortical and thalamic sections are presented as if cut from the front so that the left hemisphere is on the right part of the figure and the right hemisphere on the left part of the figure.

MK73. In cat MK73 (day 2 lesion) (See Figure 13), the cortical reconstruction shows complete removal of areas 17 and 18 on both sides except for the cortical area that represents

the upper visual field beyond 30° in area 17 and beyond 40° in area 18. There is extensive damage to area 19. In the left hemisphere, only the peripheral superior field (beyond 25°) is spared. On the right, in addition to upper and lower visual field sparing, there appears to be sparing of the central field along the vertical meridian (which is represented laterally in area 19). A small invasion of area 21A and PMLS is observed in the left hemisphere. In this cat there is very dense retrograde degeneration of all laminae in LGN and of MIN: the nuclei are characterized by very light staining, very shrunken cells, and an absence of laminar divisions in LGN. In the degenerated regions, only glia cells are present together with sparsely scattered abnormally large dark cells. Degeneration is severe in layers A and A1 in most of the nucleus except for a small but distinct region of sparing observed in the posterior 1/5th of laminae A and A1 which corresponds to the far upper field. The degeneration in the layer C and MIN is severe anteriorly but light to moderate in their posterior half which corresponds to sparing in the upper visual field of area 19. The pulvinar is intact except for the presence of shrunken cells in some of the most anterior parts of the nucleus.

MK91. Cortical reconstruction in MK91 (day 1 lesion) (Figure 14) indicates that the representation of the lower visual field is almost completely removed in areas 17 and

FIGURE 13. Diagram of the lesion extent in cat MK73. The Figure shows a surface view of the lesion extent (dotted area), coronal sections through the cortex and pattern of degeneration in the LGN. Coronal sections and LGN are shown as if cut from the front so that the right hemisphere is on the left side and the left hemisphere on the right side. In the cortex, black area: lesioned tissue. In the LGN, black area: severe degeneration, striped area: light to moderate atrophy, white area: normal.

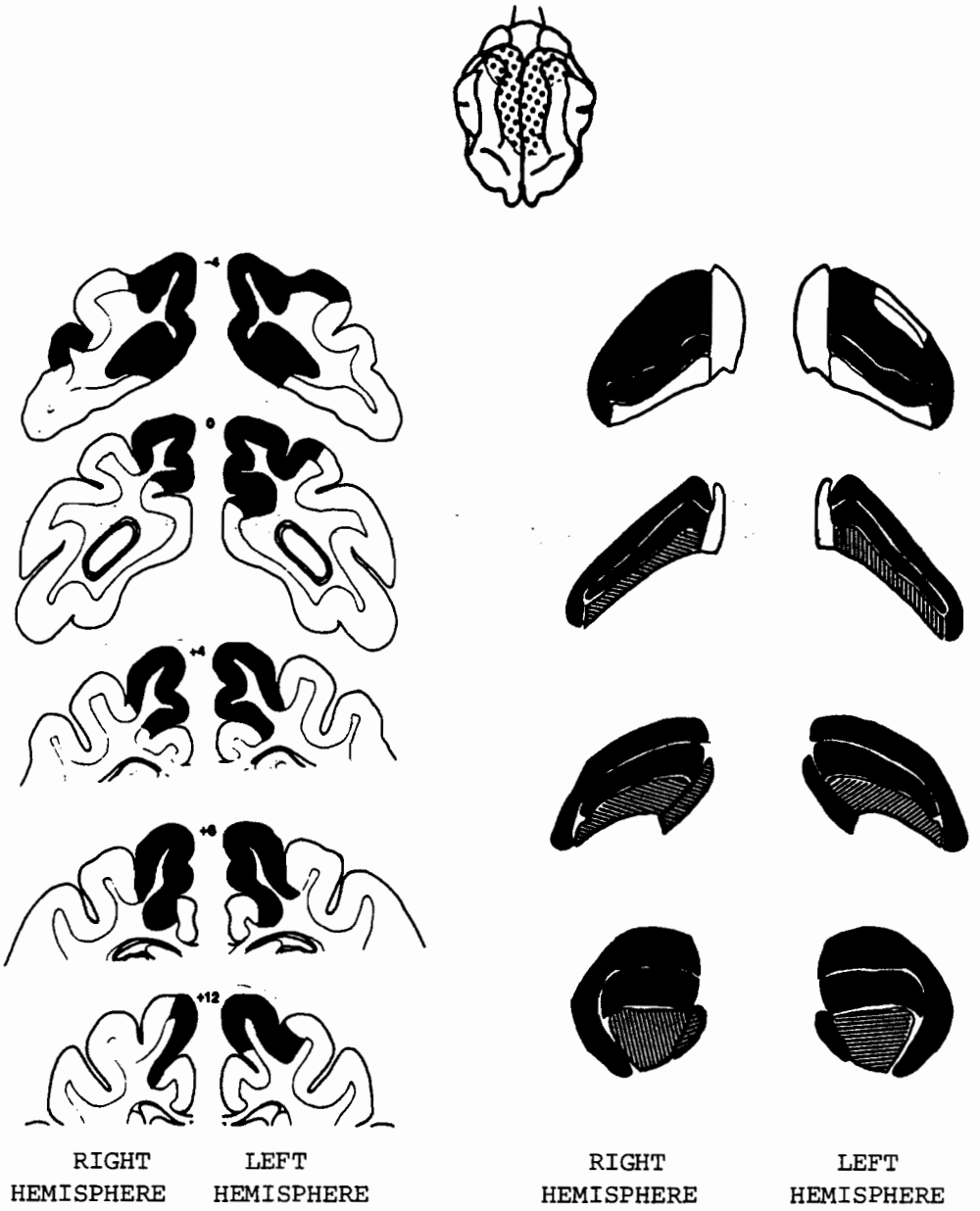
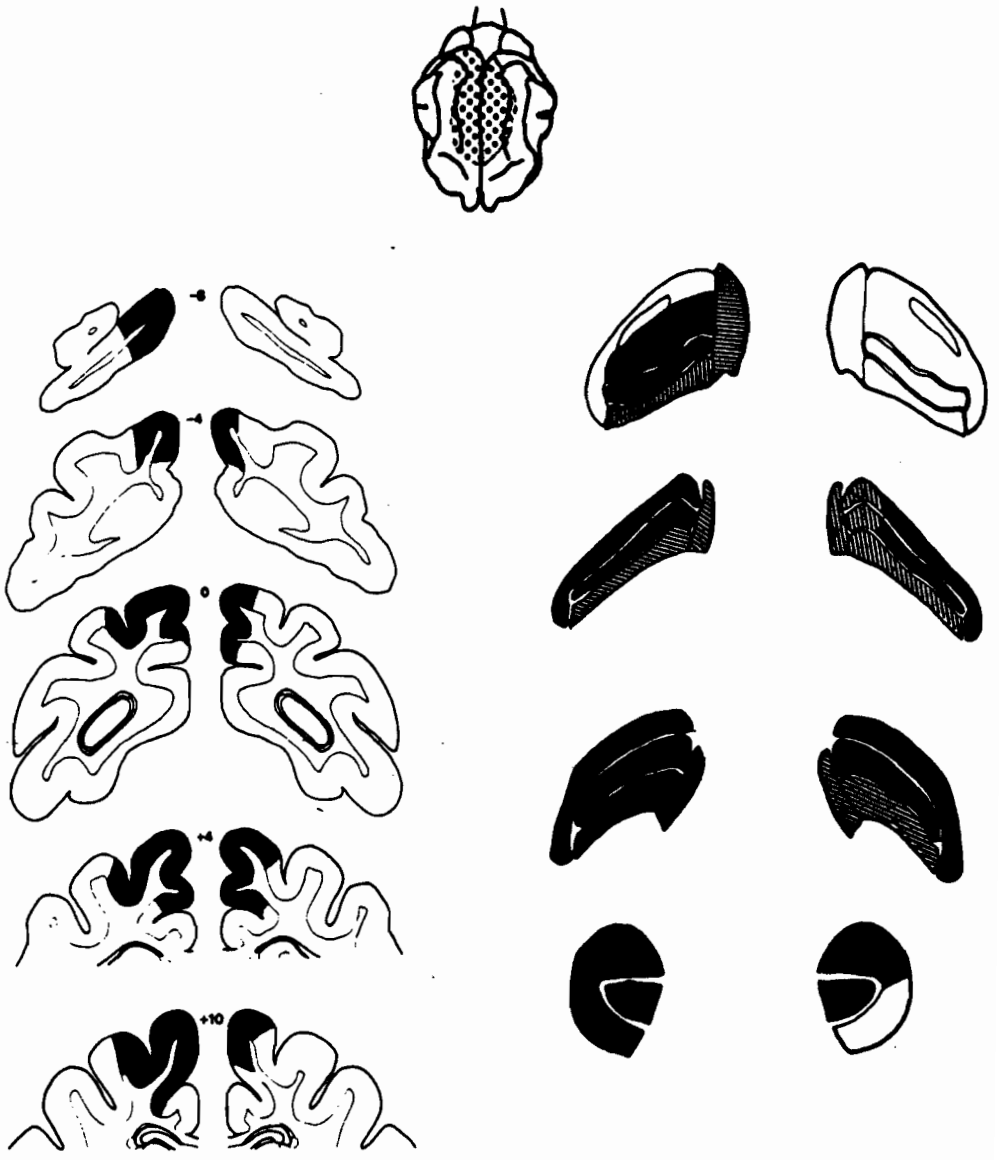


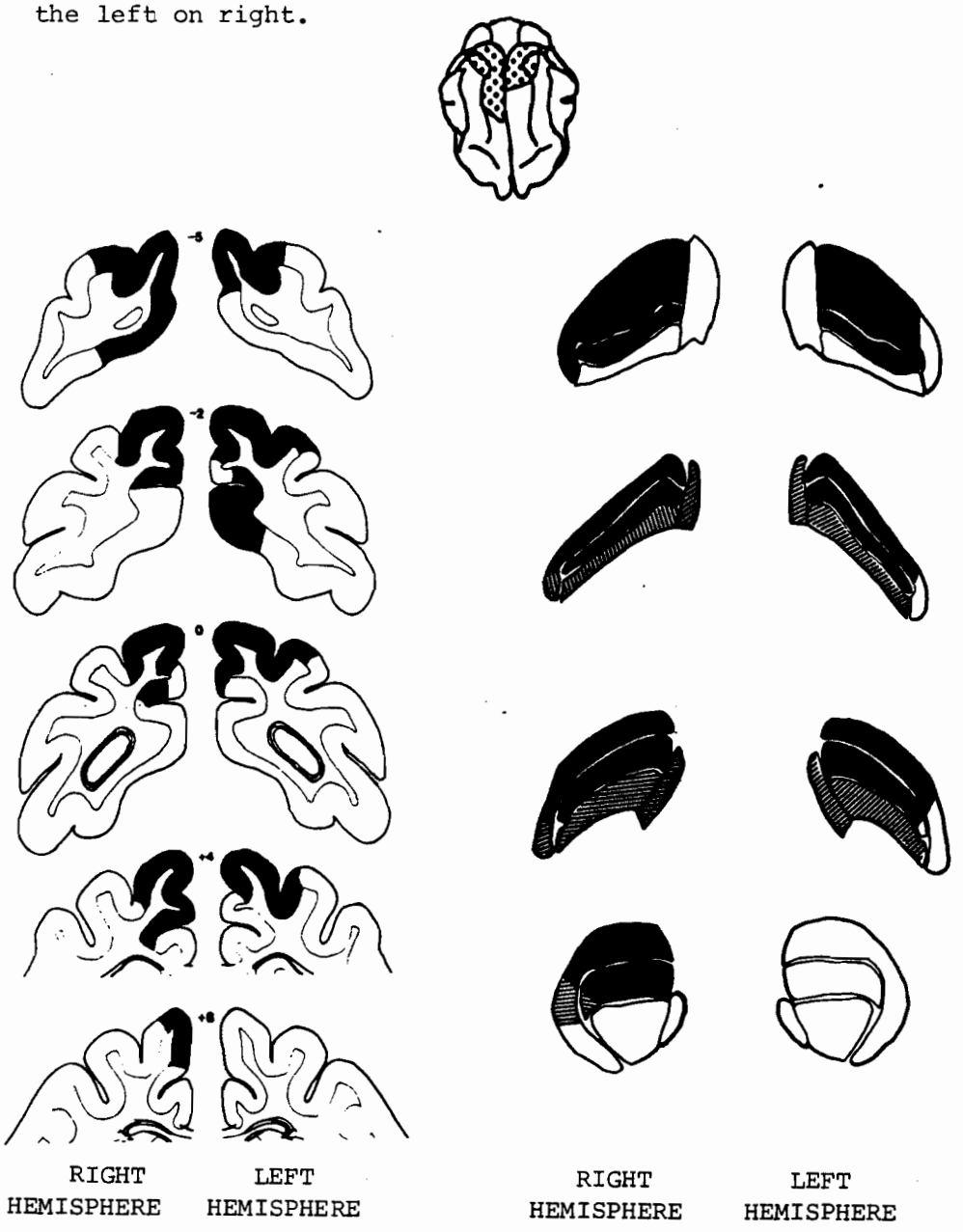
FIGURE 14. Diagram of the lesion extent in cat MK91. The Figure shows a surface view of the lesion extent (dotted area), coronal sections through the cortex (numbers indicate the level on the sagital plane), and pattern of degeneration in the LGN. Coronal sections and LGN are shown as if cut from the front so that the right hemisphere appears on the left side and the left hemisphere on the right side. In the cortex, black area: lesioned tissue. In the LGN, black area: severe degeneration, striped area: light to moderate degeneration, white area: normal.



18. There is damage to the representation of the upper visual field up to about 10° eccentricity in 17 and 18 in the right hemisphere and up to about 2° in the left hemisphere. In area 19, the lesion includes the central and lower fields on the right hemisphere but only minor damage to the lower field on the left. In this cat, the LGN is less severely degenerated than in MK73. Normal cells are encountered in the posterior parts of the LGN especially on left. There is also a small but distinct region of sparing observed on the medial aspect of laminae A and A1 in the midportion of the left nucleus which probably reflects sparing of area 18. In the more anterior part of the nucleus, severe degeneration was found in all laminae except in that part of lamina A which represents the far upper field on the left hemisphere. There is light to moderate atrophy in MIN and the deep layers of LGN except in the right hemisphere where the degeneration is severe. There are small areas in the anterior portion of the pulvinar representing parts of the lower field which show light atrophy.

MK92. In this cat (day 4 lesion, Figure 15), the cortical reconstruction indicates damage to areas 17 and 18 up to about 20° and 30° out on both sides and down to about 20° in the left hemisphere and 35° in the right hemisphere. Damage to area 19 is extensive in the left hemisphere sparing only the far superior and inferior field. Damage to area 19 in the right hemisphere is

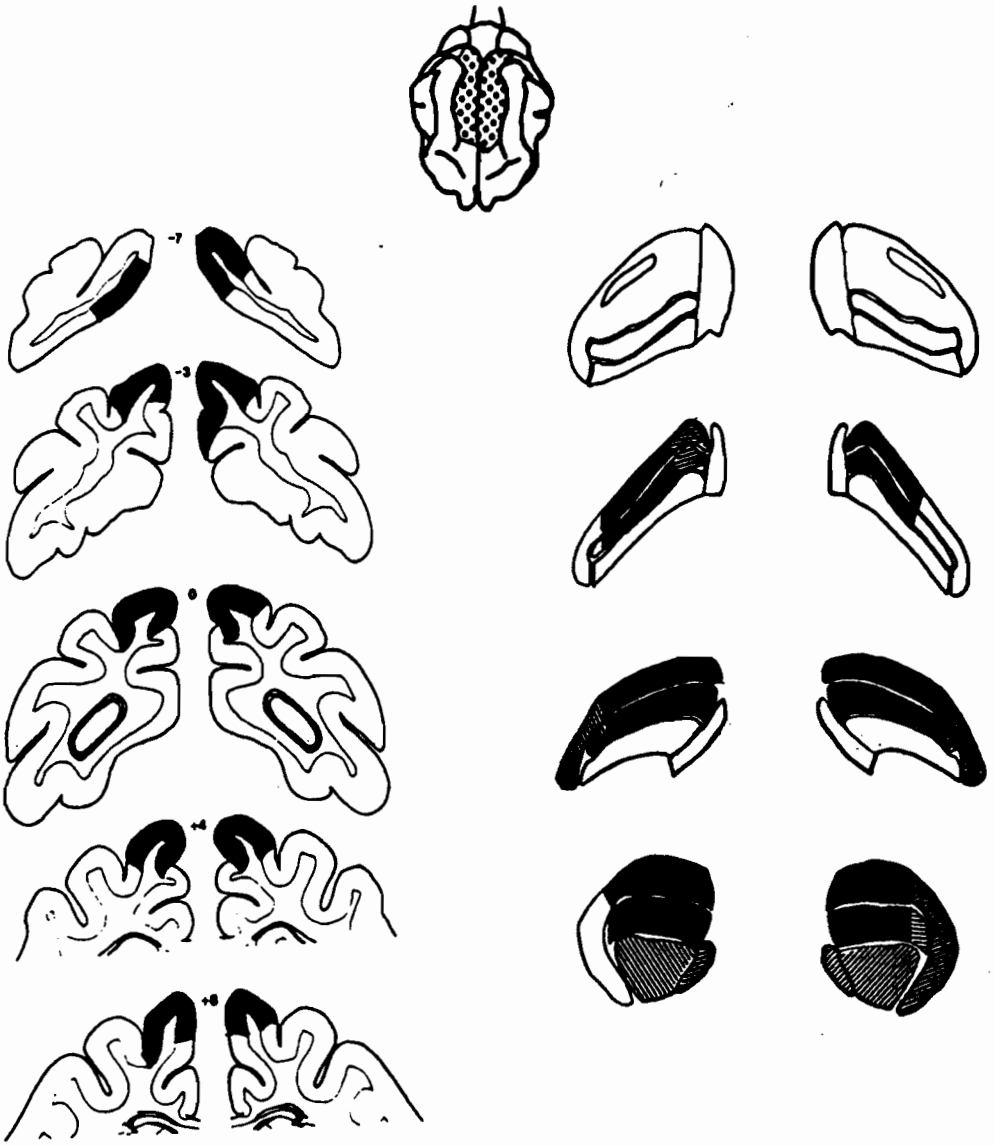
FIGURE 15. Diagram of the lesion extent in cat MK92. The Figure shows a surface view of the lesion extent (dotted area), coronal sections through the cortex (numbers indicate the level on the sagital plane) and pattern of degeneration in the LGN. In the cortex, dark area: lesioned tissue. In the LGN, dark area: severe degeneration, striped: light to moderate degeneration, white: normal. Coronal sections and LGN are shown as if cut from front so that the right hemisphere is on left and the left on right.



milder consisting mainly of the loss of the peripheral fields represented along the area 18-19 border. There is also minor damage to area 21a (central field) in the left hemisphere. The LGN shows severe atrophy. Laminae A and A1 show severe atrophy throughout except for the far lateral part which represents the monocular crescent and the lower visual field on left. The deep layers and MIN show light to moderate degeneration in the central portions of the nucleus. Finally, the pulvinar is normal.

MK95. In cat MK95 (day 8 lesion) (Figure 16) the central portion of areas 17 and 18 has been removed as well as most of the lower visual field along the vertical meridian. However, there is sparing of the cortex (17-18) that represents most of the upper visual field. The lower visual field representation in area 17 beyond 30-40^{o} was also left intact. Area 19 is essentially intact except for a small incursion into the portion that represents the lower visual fields (>40^{o} below the horizontal meridian). In this cat, the laminar pattern of the LGN is more apparent than in the other neonatally lesioned cats. Degeneration is, however, severe in laminae A and A1 especially in the anterior portion of the LGN which represents the lower visual field. Degeneration is less apparent in the deep laminae and MIN except for moderate atrophy in the anterior portion that represents the far lower visual field. No degeneration is found

FIGURE 16. Diagram of the lesion extent in cat MK95. The Figure shows a surface view of the lesion extent (dotted area), coronal sections through cortex and degeneration in the LGN. Lesioned tissue on coronalsections is indicated in black.In the LGN, severe atrophy is shown in black, striped area indicates light to moderate atrophy, white area indicates normal cells. Coronal sections and LGN are shown as if cut from the front so that the right hemisphere is on the left side and the left hemisphere on the right side.



in the posterior part of the LGN. Cells in MIN appear normal throughout. Cells in the pulvinar are normal. The lesion in this cat most closely resembles those of the adult cats described in Chapter 4.

Behavioural Results

Table 9 shows the number of trials required by each cat to reach criterion on each transfer set of the fading-in technique. The total number of trials required to learn the complete sequence of transfer tasks are 73, 391, and 256 for the normal controls (MK93, MK94, and MK96 respectively) and 189, 333, and 374 for the lesioned animals (MK91, MK92, and MK95 respectively). For one lesioned cat (MK73) a large offset in a single line was used as the training procedure. This cat required 121 trials to criterion and 611 practice trials to reach near threshold offset sizes.

One lesioned animal (MK73) was tested only as an adult but with both the grating and single line stimuli. The vernier threshold for this cat was 17.3' on the single line series and 19.5' on the Grating 1 series (Table 10).

Figure 17 shows the development of vernier acuity in two lesioned kittens and their littermate controls. The normal kittens showed gradual improvement from initial values of 23' and 30' around 55 days of age reaching 3' and 5' at 87 and 90 days of

TABLE 9. Learning trials (excluding the criterion trials) on the Fading-in technique for the three lesioned kittens (MK91, MK92 and MK95) and their control littermates (MK93, MK94 and MK96). L: Lesioned subjet; C: control littermate. The sign (-) indicates immediate transfer.

CAT	GRATING A	GRATING B	GRATING C	GRATING 1
MK91 (L)	129	-	50	10
MK92 (L)	177	6	90	60
MK93 (C)	73	-	-	-
MK94 (C)	371	10	10	-
MK95 (L)	349	20	-	5
MK96 (C)	4	40	10	202

TABLE 10. Vernier acuity thresholds (70% cutoff) for the three lesioned animals of Experiment 4 and their control littermates using the Staircase 1 (MK73) and the Staircase 2 (MK91-MK96). L: Lesioned subject; C: Control littermate.

a.

STAIRCASE 1

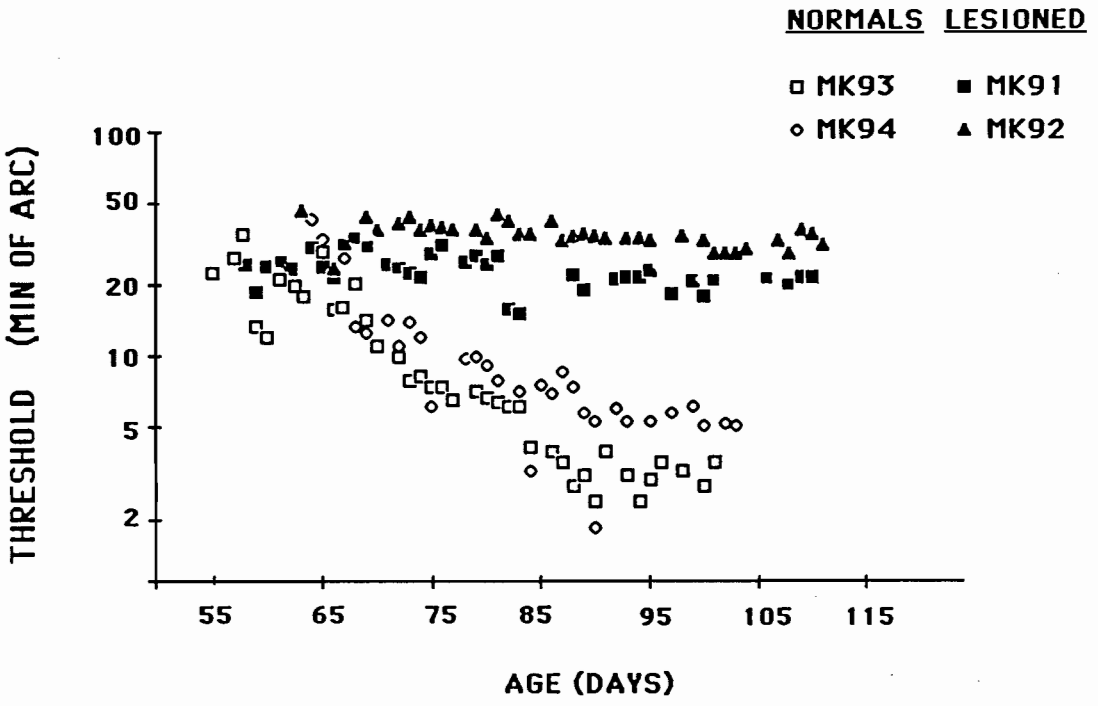
	SINGLE LINE	**GRATING 1**
MK73 (L)	17.3'	19.5'

b.

STAIRCASE 2

	GRATING 1
MK91 (L)	20.9'
MK92 (L)	29.6'
MK93 (C)	3.1'
MK94 (C)	5.2'
MK95 (L)	24.2'
MK96 (C)	4.0'

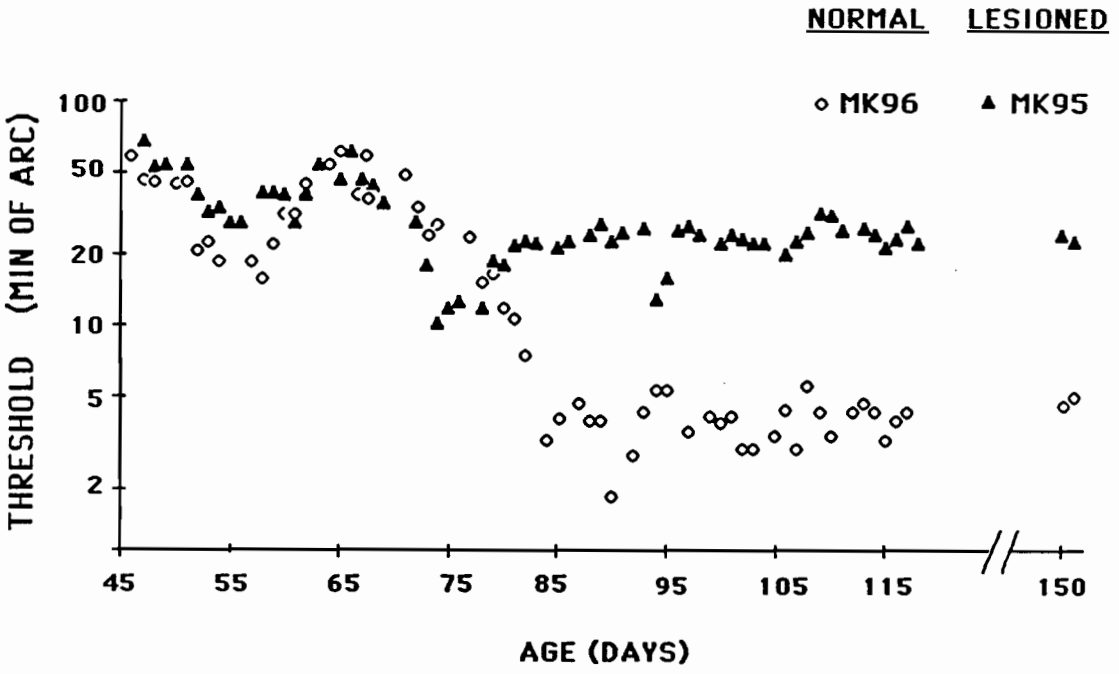
FIGURE 17. Development of vernier acuity in two lesioned kittens and their littermate controls.



age. At beginning of testing, the thresholds of the lesioned animals were 40' (62 days of age) and 25' (59 days of age) for MK91 and MK92 respectively. These initial values were close to the initial values of their control littermates. However, vernier acuity in lesioned animals did not develop as extensively as in normals during the following weeks. In the two lesioned kittens, asymptotic level is already reached 2 and 4 days after beginnning of testing (See Table 8). This threshold change during the first 2-4 days probably reflects a practice effect more than a true developmental effect. Vernier thresholds did not show any improvement below about 19' in cat MK91, and 28' in cat MK92.

A similar pattern of results was found for the remaining two kittens (Figure 18). In this case, it was possible to obtain vernier thresholds at earlier ages and therefore, some improvement is apparent in both cats. Nevertheless, vernier acuity reached stable thresholds of about 23' at 73 days in the lesioned animal, whereas its normal littermate achieved about 4' of arc at 83 days. Even after prolonged training of MK95, its vernier acuity was not different at 151 day (about 23') from the measured values at 73 days (about 19'). Daily thresholds were based on a rather small number of trials and in these two cats, there was a certain amount of intra-individual variation at beginning of testing but this disappeared quickly after threshold stabilized. The fact that the variability appears correlated in the two cats suggests that it might be related to

FIGURE 18. Development of vernier acuity in one lesioned kitten and its littermate control. These cats were tested continuously until day 151. Their thresholds on the last two days of testing are indicated.



some external factor which could not be controlled (e.g.: appetitive or aversive motivational aspects).

When measured after they reached asymptotic adult values, vernier thresholds of the normal cats were 3.1' (MK93), 5.2' (MK94) and 4.0' (MK96) (Table 10). On the other hand, the vernier thresholds measured in adulthood (>100 days) in neonatally lesioned animals were 20.9' (MK91), 29.6' (MK92) and 24.2' (MK95) (Table 10) and thus were comparable to that of MK73, tested only in adulthood.

Discussion

Like normals, lesioned animals required a large number of trials to learn the task. This is consistent with previous studies which reported normal learning of various form and pattern discrimination tasks in cats which had sustained neonatal damage to the visual cortex (Wetzel et al, 1965, Doty, 1961, Murphy et al, 1975). However, it is probable that the fading-in technique used in the present study facilitates learning by introducing a strong luminance cue on the initial training task (See A on Figure 8). It is not clear whether lesioned animals would have learned the task with such ease had the procedure used in Chapter 3 with adults been followed.

Both normal and lesioned cats generalized their learning to smaller offset sizes and performed well on the threshold task.

They showed almost perfect performance on offsets sizes well above their threshold and a rapid decrease in their performance on smaller offsets. Lesioned cats did differ from the normals in that their performance started to decline at much larger offset values.

At early ages the vernier thresholds of lesioned kittens are very close to those of normals but, contrary to normals, they develop only marginally during the following weeks and remain high. Even after an extensive training in one animal, (about 4000 trials in MK95), no threshold improvement had occurred. This indicates that the observed deficit is not the reflection of a learning problem but truly reflects a vernier acuity impairment. When measured at asymptote, the vernier thresholds of the lesioned animals were found to be 4-10 times worse than those of their normal controls. The measured deficit in the lesioned animals can not be related to the stimulus used since the single line and Grating 1 yielded very similar vernier thresholds when used in the same lesioned animal (17' and 19' on the single line and Grating 1 respectively) and in normals (Experiment 1).

Two of the lesioned cats had extensive lesions which included much of 17-18 and parts of 19, while in the other two cats, the lesions were small including mostly the central part of area 17-18. Neither the number of trials to criterion, nor the vernier thresholds varied systematically as a function of total lesion size or as a function of the extent of area 17 resection. MK95 and MK91 which sustained the smallest lesions, have

thresholds of 24' and 21', not very different from that of MK73 which sustained a large lesion that included most of area 17-18 and 19 with sparing limited to the far periphery.

Even though their thresholds were severely elevated, these cats could still perform the vernier task. There are a number of possible explanations for this residual ability. Since the lesions in three of the cats were fairly small and included only area centralis of 17 and 18, it is possible that the measured thresholds reflect performance based on spared peripheral tissue. However, cats were videotaped as they were performing the task. In the Jumping-stand like the one used here, the stimuli to which the animal has to respond are presented beneath the animal. In such conditions, an animal would have to rotate its head into an extremely peculiar position in order to use its upper peripheral field. The sparing in most of the lesioned cats was restricted to the upper visual field, and careful examination of these films did not yield evidence of any unusual head positioning. In addition, the performance level of MK73, a cat which had essentially complete removal of 17 and 18 was comparable to that of the other three cats. Another possibility which may be raised is that their performance reflects the involvement of extra-striate mechanism. Area 19 is a likely candidate since there is sparing of the central part of this area at least in one hemisphere in each of the lesioned cats. Another likely candidate is the lateral suprasylvian area.

The vernier threshold reached in adulthood does not vary as a function of the day at which the lesion was performed (day 1-2 vs day 4-8). If anything, there is slight indication that animals with later lesions perform worse (MK92, day 4, 17-18: 29.6', MK95, day 8, 17-18: 24.2') than animals with earlier lesions (MK73, day 2, 17-18-19: 19.5', MK91, day 1, 17-18: 20.9'). This is the reverse of what would be expected from the data on neonatal X-cell loss (Tong et al., 1984).

These results could be compared to the performance of cats after an adult lesion. In experiment 2, two cats with lesions relatively smaller than those of our neonatally lesioned animals showed post-operative vernier threshold of about 17'. The vernier performance observed in these two animals is very comparable to that of the neonatally lesioned cats although the lesions in the latter were larger. Damage to the very central part of area 17-18 is therefore sufficient in both neonatal and adult lesion to cause a significant impairment of vernier analysis.

These results show that cats in which cortical visual areas 17-18 or 17-18 and 19 have been removed in infancy develop poor vernier acuity. This deficit contrasts with the sparing of behavioural functions reported by a number of investigators (Doty, 1961; Murphy et al., 1975; Spear, 1979; Tucker et al., 1968; Wetzel, et al., 1965). The fact that these cats learned the task supports that conclusion. On the other hand, cats which have sustained early removal of the visual cortex are impaired on discriminating hidden figures (Cornwell et al., 1978) and on the

ability to discriminate form based on texture (Wilkinson and McCormick, 1983), two tasks which require extracting form from noise and which probably involve complex mechanisms. Severe impairment has also been reported on the ability to use stereoscopic cues to depth (Kaye and Mitchell, 1984). These tasks differ from the simple pattern and form discrimination because they all require precise spatial analysis in order to derive correct positional information. The physiological recovery that follows neonatal lesion is not adequate to subserve any of the above functions. The importance of the behavioural task used in measuring the extent of recovery after neonatal lesions should be stressed. A dramatic decrease in the sparing of function is obvious when the measure is a visual task that depends on fine positional analysis. This is probably related to the different neural mechanism that these functions reflect.

CHAPTER 7

EXPERIMENT 5: RESOLUTION ACUITY IN NORMAL AND EARLY LESIONED CATS

Resolution acuity, the ability to separate features, probably involves mechanisms different from those reflected by vernier acuity. Spear (1984) mentions that Kaye and Mitchell (personal communication) found no deficit of resolution acuity functions following neonatal damage to the visual cortex. Apart from these preliminary data there is no other report of the extent of the resolution acuity deficit after an early lesion to the visual cortex.

The question of resolution acuity deficits is complicated by the wide range of resolution acuity estimates reported in the literature (see Chapter 1). The absence of deficit in lesioned cats as compared to the controls might be explained by the use of a procedure that does not elicit optimal performance from the normal cats. In the present study, resolution acuity is measured using two types of procedures in lesioned animals and their littermate controls, for which we already have vernier acuity estimates (see previous chapter). One procedure is very similar to that used for measuring vernier acuity. The other is modelled on that used by investigators who have reported very high

resolution acuity estimates in cats (Mitchell and Murphy, personal communication to F.W.).

Method

Subjects

Resolution acuity was assessed in six adult cats. Five of these were subjects in the vernier study reported in Chapter 5. The sixth (MK74) was a normal cat from the same litter as MK73.

Stimuli and Procedure

Two techniques and stimulus sets were employed to evaluate resolution acuity thresholds.

Two littermates (MK73 and MK74) were tested with the Staircase 1 procedure, using the apparatus and lighting conditions described in Chapter 2. The stimuli were photographically produced vertical square-wave gratings 25 cm wide and 20.5 cm long. A series of 14 spatial frequencies were produced, the sizes of which ranged from 0.44 c/deg to 9.7 c/deg see Appendix 2) from a 50 cm viewing distance, the distance from which both cats were tested. From that same distance, each stimulus subtended a total area of 22^{o} by 27^{o}. The positive stimulus was a grating of a particular spatial frequency (see below) while the negative stimulus was a uniform grey field of approximately equivalent brightness. Lighter and darker grey

fields were regularly used to control for the use of luminance cues. Animals were tested on a sufficient number of days to produce about 100 trials on each spatial frequency value around threshold. Contrast value was about 0.4.

The four remaining cats were tested with a modified version of the method of limits designed to optimize resolution acuity performance. The Jumping-stand apparatus described in Chapter 2 was used except that it was painted in mat grey and was illuminated from beneath the jumping platform. The viewing distance was 57 cm for all four animals.

The stimuli consisted of a series of 53 vertical high-contrast square-wave gratings (Appendix 3) produced by photographic enlargment on semi-mat paper from Ronchi rulings. From a viewing distance of 57 cm, each stimulus subtented a total area of 18^{o} by 18^{o}. The positive stimulus was a vertical square-wave grating while the negative stimulus was a vertical square-wave grating the spatial frequency of which (above 12 c/deg) was well above the highest published estimate of cat resolution acuity threshold. Seven copies of the negative stimulus were produced and they were used alternately to avoid introduction of predictable extraneous visual cues. Luminance level was approximately 100 cd/m^2 and contrast values around 0.90.

This second procedure involved, as a first step, a rough threshold estimate using Staircase 1 (Chapter 2). Performance on this first assay determined the sequence of trials in the final

threshold delineation procedure in the following way: two series of alternating spatial frequencies were used in turn every other day. The series of 53/2 stimuli were presented one by one in order of increasing spatial frequency until the grating corresponding to the second octave away from the estimated threshold (estimated by Staircase 1). From that point, each stimulus was presented twice until the grating that corresponded to the first octave away from threshold. From that point, each stimulus was presented three times. At any point in the series, if the animal failed on one trial, the failed stimulus was presented for five consecutive trials and the animal had to achieve a 4/5 correct performance on that stimulus to continue. If the animal failed to reach that criterion, presentation of the same stimulus was continued for a total of ten trials. Testing was continued to the next highest spatial frequency if the animal succeeded on at least 7/10 trials. If the animal failed to reach 7/10, testing was discontinued for that day and this value was taken as the day's threshold. Consequently, no limit was set as to the number of trials in a single daily session but there were never more than 90 trials administered to the same cat in a day. Animals were tested on a sufficient number of days to gather about 100 trials on each value around threshold.

TABLE 11: Number of trials to criterion, number of practice trials and age at threshold measurement for the three lesioned subjects of Experiment 5 and their controls. L: Lesioned animals; C: controls.

STAIRCASE PROCEDURE

CAT	TRIALS TO CRITERION	PRACTICE TRIALS	AGE AT THRESHOLD MEASUREMENT
MK73 (L)	60	120	>4 months
MK74 (C)	30	120	>4 months

METHOD OF LIMIT

CAT	TRIALS TO CRITERION	PRACTICE TRIALS	AGE AT THRESHOLD MEASUREMENT
MK91 (L)	305	655	>4 months
MK92 (L)	130	950	>4 months
MK93 (C)	125	927	>4 months
MK94 (C)	75	893	>4 months

Results

Table 11 shows the procedure used for each cat, the number of trials to criterion, the number of practice trials and the age at threshold measurement. The lesioned cats required 60, 305, and 130 trials to learn the task (MK73, MK91, and MK92, respectively). The normal animals learned the task after 30, 125 and 75 trials (MK74, MK93, and MK94, respectively).

For each cat, the percent correct performance was plotted on a log scale against spatial frequency. A line was fitted by regression analysis to the descending portion of the resulting frequency of seeing curve. The resolution acuity threshold was taken as the spatial frequency that yielded a 70% correct performance. This technique is the same as was used to determine vernier thresholds. Table 12 shows the resolution acuity thresholds measured in the 6 cats with the method of limits and the staircase procedure. Resolution thresholds measured in normal animals were 3.6 c/deg (MK74 with the Staircase procedure), 4.1 c/deg and 4.5 c/deg (MK93 and MK94 respectively with the method of limits). On the other hand, the resolution acuity measured in the three lesioned animals were 3.6 c/deg (MK73 with the Staircase procedure), 3.0 c/deg and 3.6 c/deg (MK91 and MK92, respectively with the method of limits). It should be emphasized that the sessions were videotaped (See Chapter 2) and that the lesioned cats did not show any peculiar head position during

TABLE 12. Resolution acuity thresholds for the three lesioned animals (MK73, MK91 and MK92) and their control littermates (MK74, MK93 and MK94). L: Lesioned animal; C: control littermate.

RESOLUTION ACUITY THRESHOLD

STAIRCASE PROCEDURE

CAT

MK73 (L)	3.6 C/DEG
MK74 (C)	3.6 C/DEG

METHOD OF LIMIT

CAT

MK91 (L)	3.0 C/DEG
MK92 (L)	3.6 C/DEG
MK93 (C)	4.1 C/DEG
MK94 (C)	4.5 C/DEG

training or testing. It is therefore unlikely that they were using cortical remnants to perform the task.

Discussion

Although they required twice as many trials than their littermates, lesioned animals were able to learn the task and, when they had mastered it, they transferred easily to higher spatial frequencies. In general, they performed at better than 90% correct on low spatial frequencies and rapidly dropped to near chance level at high spatial frequencies.

Resolution acuity thresholds for the normal cats range from 3.6 c/deg to 4.5 c/deg. The two procedures used to delineate thresholds yielded fairly similar values (3.6 c/deg with the staircase procedure and 4.1 and 4.5 c/deg with the method of limits), though there was a tendency for the method of limits to yield slightly better acuity estimates. These thresholds are, however, still lower than the 8 c/deg measured by Giffin and Mitchell (1978) with a similar procedure. It is not clear why the same procedure used in two different laboratories yields such a dramatically different range of thresholds. A possible explanation may lie in the amount of practice in the task. A large number of trials were given to the animals before their thresholds were measured but slight improvements were still observed throughout testing. It is therefore possible that a more

prolonged testing might have yielded higher threshold estimates. However, the observed improvements were very slight and it is unlikely that they would be sufficient to allow values as high as 8 c/deg to be reached, even after a larger number of trials. Other factors which are known to influence resolution acuity are luminance level, pupil size and contrast level. Some of these could partly account for the observed discrepancy between the present result and that of Giffin and Mitchell (1978). However, luminance and pupil size are probably not critically involved since a three-day trial run was done in a bright daylit room and no threshold differences were observed. In addition, the contrast level in our second set of grating stimuli was almost identical to that of Giffin's stimuli (almost 1 vs. 0.9 in this experiment). Nevertheless, if we compare the resolution acuity values reported here to other estimates from the literature (see Chapter 1), the present thresholds are within the reported range of normal cat acuity thresholds (Blake et al, 1974; Elberger, 1982; Mitchell et al., 1976, 1977; Muir and Mitchell, 1975; Pasternak and Merigan, 1981; Smith, 1936).

When measured in lesioned animals, resolution acuity values ranged between 3.0 and 3.6 c/deg. The two lesioned cats tested with the method of limits had slightly worse resolution acuity than their littermate controls (20-30% worse). Their lesions were small and there was spared tissue in area 17-18. It is therefore possible that they were using peripheral field to perform the task. However, no threshold differences were found between the

lesioned cat tested with the Staircase procedure and its control littermate (3.6 c/deg) even though the lesion was very large (17-18-19) and the sparing limited to the very far periphery. Even if the procedure did not yield optimal performance from the control littermates, the data suggest that resolution acuity was relatively little affected by a striate cortex removal. It is noteworthy that the threshold values reported in the three lesioned animals remain in the range of normal cat resolution acuity typically measured in this laboratory (3-5 c/deg) and reported by other investigators (3-9 c/deg; Blake et al., 1974, Elberger, 1982; Mitchell et al., 1976, 1977; Muir and Mitchell, 1975; Pasternak and Merigan, 1981; Smith, 1936). For this reason, it is not clear whether the observed differences reflect individual variations or real deficits. In fact, if there is a resolution acuity deficit following an early removal of the visual cortex (areas 17-18 or 17-18-19), this deficit remains relatively minor and is comparable to or slightly less severe than the deficit observed (25-30% increase) following an adult lesion (Berkley et al., 1979; Sprague and Berkley, 1979; Sprague et al., 1981).

CHAPTER 7

GENERAL DISCUSSION

The present set of studies investigated various aspects of vernier acuity in cats. The first experiment showed that vernier acuity in normal adult cats ranges from 2 to 5' and that it is quite resistant to the psychophysical procedure and to variation in certain of the stimulus parameters. Experiment 2 confirmed the involvment of striate cortex in cat vernier acuity by showing severe post-operative deficits following a removal in adulthood of the representation of the central visual field. In experiments 3 and 4, the development of vernier acuity was documented in normal kittens and in kittens which had sustained a neonatal removal of the visual cortex representing the central visual field. In normal kittens, vernier acuity developed quite rapidly from initial values of about 40' to 2-5' before 90 days of age. In early lesioned animals, vernier acuity thresholds remained high and did not get better than about 20' even after prolonged testing. Finally, Experiment 5 examined resolution acuity in cats which had sustained neonatal visual cortex damage and in littermate controls. Resolution acuity is 3.6 to 4.5 c/deg in the normals and 3.0 to 3.6 c/deg in lesioned cats. These estimates are all within the range of normal resolution thresholds.

Hyperacuity in normal cats

One of the questions which motivated Experiment 1 was whether cats, like humans, exhibit hyperacuity. It was found that cat vernier thresholds range from 2' to about 5' of arc. The same range of values was found in Experiment 3 with another group of cats. In Experiment 3, values as low as 1.5' were measured.

In humans, vernier acuity is called a hyperacuity because it is better than the resolution of the system assessed both by the optical resolving power of the eye, the intercone distance and by the behavioural resolution acuity (Westheimer, 1979). In cats, the optical resolution of the eye corresponds to the intercone distance but the resolution acuity is worse than what would be expected based on these two measures. However, in the cat retina, a high degree of convergence exists between cones and ganglion cells even at the area centralis (Hughes, 1975; Steinberg et al., 1973; Stone, 1965) and the limits of resolution acuity have been related to inter-ganglion cell distance rather than to the inter-cone spacing (Hughes, 1981, Wassle et al., 1981).

A hyperacuity is defined in relation to the resolving capacity of a visual system. In order to estimate the extent of cat hyperacuity, their vernier thresholds should be compared to their resolution acuity since this is the limiting measure. Cat resolution acuity has been estimated in a number of studies and values ranging from about 3 to 9 c/deg have been reported (Blake

et al., 1974, Muir and Mitchell, 1975, Giffin and Mitchell, 1978; Jacobson et al, 1976; Mitchell et al., 1976, 1977; Muir and Mitchell, 1975; Pasternak and Merigan, 1981; Smith, 1936). In order to compare resolution and vernier acuity, resolution acuity values are converted to the half-period at threshold in minutes of arc (this corresponds to the Nyquist limit). To be defined as a hyperacuity, vernier thresholds would have to be lower than 3.3' if compared to the best resolution cutoff estimate (Jacobson et al., 1976), lower than 5' if compared to an average cutoff (Blake et al., 1974) and lower than 10' if compared to a low cutoff (Pasternak and Merigan, 1981).

Inter-study comparisons of the two types of acuity is not an ideal procedure because it introduces much uncertainty as to the comparability of measures. Ideally, comparisons should be based on the measurement of both acuities (resolution acuity and vernier acuity) carried out under similar laboratory conditions and, at best, within the same animals. Berkley and Bush (1983) report vernier acuity thresholds in normal cats in which resolution acuity had also been measured. Vernier thresholds measured in their normal subjects were either equal to resolution acuity (7.7':vernier vs 7.5':resolution and 5':vernier vs 6':resolution) or slightly worse (8':vernier vs 6.6':resolution). This implies that no interpolation process is used to extract offset information in the cat visual system. It should however be remembered that the behavioural paradigm used by Berkley and Bush

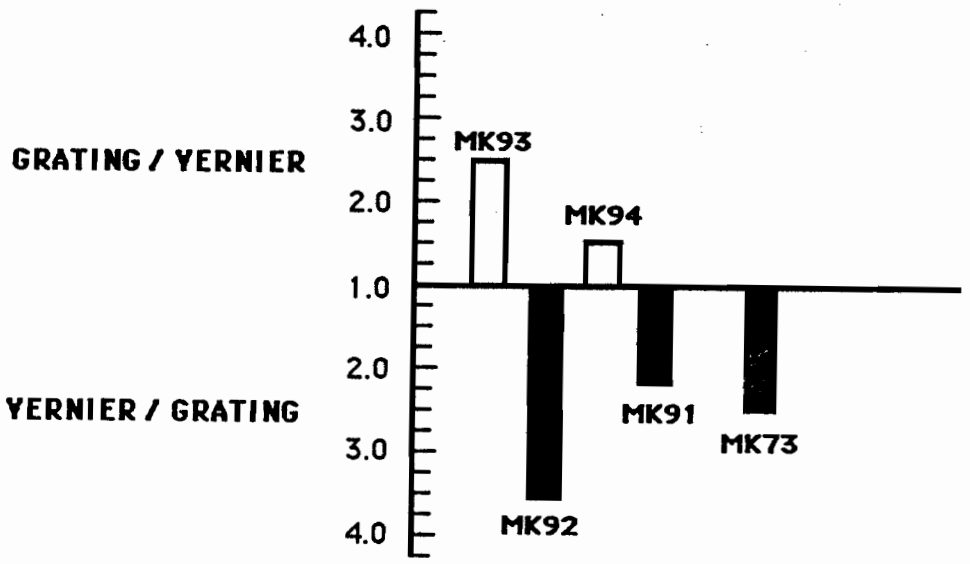
may have lacked the salience necessary to elicit optimal performance from cats on the vernier task.

Experiments 4 and 5 report measurements of vernier and resolution acuity performed in the same animals in an attempt to test directly whether cat vernier acuity is finer than resolution acuity. In the two visually intact cats tested on both measures, resolution acuity thresholds were 7.3' (4.1 c/deg) and 6.6' (4.5 c/deg) whereas the vernier thresholds were 3.1' and 5.2' respectively (See Summary Figure 19). Thus, in one of the two animals vernier acuity is more than two times better than resolution acuity. The vernier acuity of the other cat is, however, only slightly better than its resolution acuity. These resolution acuity values are representative of the range of acuity values measured in our laboratory under similar testing conditions.

If the range of vernier acuity thresholds measured in all the normal cats included in the present set of studies (1.6' to about 5') is compared to the resolution acuity values reported in Experiment 5 (8.6' to 6.6') there is strong suggestion for the presence of interpolation in the cat visual system. The magnitude of this interpolation is a 2- to 5-fold increase. These results suggest that vernier acuity is a hyperacuity in cats but that the magnitude of the interpolation is much inferior to that found in humans and does not exceed a factor of five.

Stereoacuity is another hyperacuity in humans. It is interesting to note that cats' stereoacuity thresholds are very

FIGURE 19. This Figure compares resolution thresholds to vernier thresholds in normal (light bars) and neonatally lesioned (dark bars) cats. In normals, the Figure shows resolution acuity (grating) over vernier acuity. In lesioned cats, the Figure shows vernier acuity over resolution acuity. A result of 1.0 would indicate that both acuities have the same threshold values in that particular cat.



similar to vernier acuity thresholds (4' to 10') (Blake and Hirsch, 1975; Kaye et al., 1981; Timney, 1981, 1983, 1984). Consequently, two abilities that are hyperacuities in humans are limited to the same extent in cats. However, the human literature provides evidence that these two abilities reflect different mechanisms (Berry, 1948, Stigmar, 1970, Westheimer and McKee, 1979) and this might also be the case in cats. In terms of physiological substrates, disparity tuned cells are presumed to be involved in the processing of stereoacuity but there is no reason to suppose that the analysis of disparity is related to the detection of misalignment. There is no report as to whether the vernier cells described in the cortex by Swindale and Cynader (1986) show any disparity tuning. This should certainly be documented further. Nevertheless, this common limit of vernier and stereoacuity found in cats reinforces the suggestion of a common pool of fine-grained spatial information at an early stage of processing (Berry, 1948; Stigmar, 1970).

How can one account for the relatively smaller amount of interpolation in the cat visual system as compared to humans? Striate cortex, more specifically Layer IVC , the input target of X-cells, has been related to interpolation in vernier acuity. The convergence of relatively few geniculate fibers onto a much larger number of densely packed cells in layer IVC of the primate has suggested its involvement in an interpolation process (Barlow, 1979a, b, 1981; Crick et al., 1981). Experiment 2 shows that in adult cats, a removal of the representation of the area

centralis in 17-18 is sufficient to seriously disrupt vernier acuity. This confirms the findings of Berkley and his collaborators (Berkley and Sprague, 1979; Sprague et al., 1979; Berkley and Bush, 1983) which have demonstrated deficits in detecting vernier offsets after both central field lesions and slicing in areas 17 and 18. Striate cortex is therefore most likely involved in the processing of cat vernier acuity. In cats, the ratio of geniculate neurons to target cells in area 17 is much smaller than in primates. Beaulieu and Colonnier (1983) estimate 1/20 in cats (Layer IV) and 1/55 in monkeys (Layer IVA and IVC). Furthermore, the receptive field properties of the units in layer IV differ in the two species. In cats, the cells which receive direct X-cell input are predominantly simple cells with elongated receptive fields (Bullier and Henry, 1979; Gilbert and Wiesel, 1979). On the other hand, the cells of Layer IVC in the primate have receptive field properties similar to that of geniculate neurons: they have nonoriented receptive fields and are monocularly activated (Blasdel and Fitzpatrick, 1984; Hubel and Wiesel, 1968, 1977). Such characteristics would be desirable for a fine-grained reconstruction of the visual information by allowing direct reproduction of the thalamic input at the cortical level but on a much finer scale. These differences at the cortical level between the cat and primate could account for the more modest degree of interpolation which is suggested by our data.

The development of vernier acuity in normal cats

The normal development of vernier acuity was investigated in Experiment 3. Vernier acuity was found to develop quite rapidly between 45 and 80 days. This developmental rate contrasts with the slower development of resolution acuity which reaches adult level at about 110 days of age (Giffin and Mitchell, 1978; Mitchell et al., 1976). However, the development of vernier acuity parallels that of stereoacuity (Timney, 1981, 1983, 1984). Interestingly, in humans, the development of vernier acuity also parallels that of stereoacuity and differs from that of resolution acuity (Shimojo et al., 1984). The remarkable parallel between the development of vernier acuity relative to other acuities in human and cats suggests that even if vernier acuity does not reach as high relative values in cats as in humans, it may reflect qualitatively similar mechanisms. As a consequence, cats can provide a valuable non-human model for the study of the neural mechanism of vernier acuity. The data also support the suggestion that vernier acuity and resolution acuity do not reflect the same physiological mechanisms. Shimojo and Held (1987) recently suggested that the development of vernier acuity may depend on the changes in the density of the receptive fields (i.e. the number of receptive fields per unit area of visual field which would actually determine the mean sampling distance. The development of resolution acuity would depend on the

development of the receptive field centre size according to these authors.

On the other hand, stereoacuity and vernier acuity might have commonalities since they develop at similar rate (Timney, 1981, 1983, 1984). In terms of development, the onset of stereopsis in kittens has been linked to the appearance of disparity tuned cells and the development of stereoacuity during the following weeks related to the development of the tuning of disparity selective cells (Mitchell and Timney, 1982, 1984; Timney, 1981, 1983). However, as was previously mentioned, both acuities might share common substrates in their early stages of processing (Berry, 1948; Stigmar, 1970). It is possible that the developmental rate common to the two acuities relates to the development of this mechanism. Alternatively, if the development of stereoacuity is related to the development of neuronal disparity sensitivity, that of vernier acuity might be related to the development of the spatial displacement sensivity observed in cortical units (Swindale and Cynader, 1986). In that case, the development of the fine tuning in both abilities may have similar requirements at the single-cell level (e.g. precisely defined receptive fields, strong inhibitory surround) which would develop more or less at the same rate in both types of cells.

The development of vernier acuity after a neonatal lesion

The development of vernier acuity was also investigated in kittens which had sustained an early removal of the visual cortex (Experiment 4). Within the time period that could be studied, there was no evidence of vernier development in any of the three lesioned kittens. The threshold improvement with age was marginal and never reached the amplitude seen in normal animals (1.5-2 times better in lesioned animals compared to a 10-fold improvement in normals). It would have been conceivable to observe in lesioned animals a developmental rate parallel to that of normals but with higher threshold values. The fact that this was not the case suggests that the physiological mechanism which is involved in lesioned animals' vernier acuity undergoes little developmental change, at least in the time period investigated. The fact that the lesioned animals could solve the vernier problem with large offsets thus meeting the basic demand of the vernier task implies the participation of a neurophysiological mechanism that has spatial properties. However, the present data suggest that by 60-70 days, this mechanism has reached its full development. It is important to stress that the present data do not provide answers as to the development of this mechanism prior beginning of our testing (about 60 days). It remains unclear whether some development would have been highlighted at earlier

ages if vernier measurements had been possible. To access this time period the use of different procedures such as the preferential looking technique (Sireteanu, 1986) could prove useful.

Vernier thresholds measured in neonatally lesioned cats when they reached adulthood ranged from 17' to 30' of arc. This is consistent with previous reports which showed an impairment of stereopsis, texture segregation and complex visual discrimination after early visual cortex damage (Cornwell et al., 1978; Kaye et al., 1982; Wilkinson and McCormick, 1984). Despite anatomical and physiological reorganization following early visual cortex damage, marked retrograde degeneration of the LGN, the loss of its fine-grained topological organization and transneuronal degeneration of retinal ganglion cells have been observed (Kalil, 1980; Spear et al., 1980b). The degenerated retinal ganglion cells are essentially X-cells, the density of which is greatly reduced. The impairment in vernier acuity observed after an early lesion of the visual cortex may be related to the decreased density in the sampling of the visual information which would appear consistent with the recent hypothesis that the development of vernier acuity is dependent on the development of the density of the receptive fields at a peripheral level (Shimojo and Held, 1987). However, the degeneration of the X-cells is much more extensive when the lesion is performed on the day of birth than at 14 days or later (Kalil, 1980; Pearson et al., 1981; Tong et al., 1984) and in this study, a lesion made on day 1 did not

yield worse vernier thresholds (MK91: 20.9') than when made at later ages (day 2- MK73: 19.5'; day 4- MK92: 29.6, day 8- MK95: 24.2'). This suggests that the degrees of X-cell loss may not be the most critical factor in the deficit. Of course, since intermediate ages (between 1 and 14 days) have not been anatomically and physiologically documented, this conclusion depends on the assumption that lesions done at such ages result in intermediate degree of degeneration of X-cells. Among other factors which could be involved in the observed deficits are the characteristics of units in LS, i.e. the new target of X-cells. The cells in LS have large receptive fields and a loose topographic representation (Spear et al., 1980a, Tong et al., 1984). These properties do not seem appropriate to suppport good vernier acuity. The high degree of positional specificity and fine spatial tuning of the cells that normally constitute the removed cortex appear necessary to support fine grained visual abilities.

Hyperacuity after a neonatal lesion

Vernier and resolution acuity were measured in the same paradigm in two lesioned cats and their control littermates in order to see if the superiority of vernier over resolution acuity is preserved following a neonatal lesion. Whereas vernier acuity was seriously disrupted by a neonatal damage to 17-18, resolution

acuity remained relatively unaffected. In normal cats, vernier acuity is better than resolution acuity but in the neonatally lesioned cats vernier acuity (17-30') was found to be much worse than resolution acuity (8-10') (See Summary Figure 19). This observation implies that the mechanisms which support good resolution acuity in lesioned animals can not support vernier acuity to an equivalent extent. Note that a similar dissociation has been observed after an adult lesion (Berkley et al., 1979; Sprague and Berkley., 1979). A similar relationship, i.e. worse vernier acuity than resolution acuity, is also seen during very early development in human infants. This again confirms that they involve different neural substrates and that each develops at its own rate.

Lesions performed in adult cats yielded comparable vernier deficits. Since we did not measure their resolution acuity, we can not draw any conclusion about the degree of hyperacuity in these cats and hence, whether there is relatively greater sparing of vernier acuity after an early lesion than there would be after an adult lesion. But we can say that the deficit observed in vernier acuity is more severe than that observed in resolution acuity in the neonatal lesions and in that sense, the neural plasticity that follows an early visual cortex removal is task-specific.

Models of vernier acuity

One of the implications of the findings of the present study is that in cat, as has been suggested in humans, different mechanisms participate in resolution acuity and offset detection. This raises questions as to the relevance of defining vernier acuity in relation to resolution acuity. Watt (1984) proposed that resolution and vernier acuity are not only quantitatively but also qualitatively different and subject to different rules (this is illustrated by the fact that in some conditions vernier acuity is relatively resistant to blur (Westheimer, 1979)). Watt (1984) proposed that resolution acuity might reflect a mechanism that is responsible for analysing the nature (quality) of the stimulus whereas vernier might reflect a mechanism involved in the analysis of the spatial location of objects and the relation among them. It is interesting to observe that vernier acuity is an ability which is relatively resistant to stimulus variations but is dependent on the integrity of striate cortex whereas the reverse is true for resolution acuity.

The present results may shed some light on the characteristics of the physiological mechanism that participates in offset detection. Neuronal hyperacuity has been observed in units of area 17 (Swindale and Cynader, 1986) and it was suggested by these authors that they underlie vernier acuity. The present set of data raise a number of unanswered questions

concerning these neural vernier units and one of them is whether in normal cats, these develop their sensitivity in parallel to behaviourally measured vernier acuity. If this is so, it would certainly strengthen the suggestion that they are involved in vernier acuity processing. It is as yet unknown whether cells in normal LS show the same sensitivity to offset displacement. If the offset detection measured in our early lesioned cats reflects the involvment of extra-striate mechanisms it is obvious that the precision reached is far less than in the striate cortex even with the possible benefit of "neonatal plasticity".

The multi-mechanism approach to hyperacuity strongly suggests that more than one mechanism is involved in hyperacuity. In humans, the access of all mechanisms to a common pool of information would, however, allow a coding that would be equivalent in terms of efficiency across mechanisms. It has been proposed that vernier acuity is processed by orthoaxial information analysis which would integrate information across space and would be involved in edge detection and contour shape processing in the first stage of the analysis of a visual scene. Other types of hyperacuity are subject to different rules and restrictions and are probably processed by different physiological mechanisms. It would be interesting to extend the examination of these abilities in cats especially since it is in this species that the physiological substrate of hyperacuity is best known. In particular, it would be important to examine the ability of the cat to perform tasks which seem to reflect other

types of coding operations in humans (e.g., chevron and curvature analysis). In order to further specify the characteristics of the coding processes involved in cat acuities, the effects of the stimulus parameters such as blur, contrast and movement should also be examined systematically. It would be particularly interesting to investigate other tasks which involve a different mechanism and are less affected by decreased sampling (e.g. two-dot acuity) in developing cats and in cats which had sustained neonatal visual cortex damage. A knowledge of the extent to which normal and lesioned cats can rely on other types of spatial coding operations would certainly provide insight as to their physiological organization and requirements.

APPENDIX 1

Offset sizes in the vernier stimuli given in millimeters and in minutes of arc. The angular measurements are based on 6 different viewing distances. The abbreviation G1 stands for Grating 1, G2 for Grating 2 and S for the single line. The number that follows the abbreviation represents the number of the stimulus in the series.

STIMULUS	SIZE (mm)	DISTANCE					
		250mm	300mm	400mm	470mm	500mm	750mm
G1-1	7.20	99	84	62	52.6	49.5	33
G1-2	6.24	85.8	72	53.6	45.6	42.9	28.6
G1-3	5.44	75	61.8	46.8	39.8	37.4	24.9
G1-4	4.80	66	55	41.3	35.1	33	22
G1-5	4.16	57.2	47.7	35.8	30.4	28.6	21.1
G1-6	3.60	49.5	41.3	30.9	26.3	24.8	16.5
G1-7	2.96	40.7	33.9	25.4	21.7	20.4	13.6
G1-8	2.40	33	27.5	20.6	17.6	16.5	11
G1-9	2.00	27.5	22.9	17.2	14.6	13.8	9.2
G1-10	1.68	23.1	19.3	14.4	12.3	11.6	7.7
G1-11	1.44	19.8	16.5	12.4	10.5	9.9	6.6
G1-12	1.28	17.2	14.7	11	9.4	8.8	5.9
G1-13	1.12	15.4	12.8	9.6	8.2	7.7	5.1
G1-14	0.96	13.2	11	8.3	7	6.6	4.4
G1-15	0.80	11	9.2	6.9	5.9	5.5	3.7
G1-16	0.64	8.8	7.3	5.5	4.7	4.4	2.9
G1-17	0.48	6.6	5.5	4.1	3.5	3.3	2.2
G1-18	0.32	4.4	3.7	2.8	2.3	2.2	1.5
G1-19	0.16	2.2	1.8	1.4	1.2	1.1	0.7

STIMULUS	SIZE (mm)	DISTANCE					
		250mm	300mm	400mm	470mm	500mm	750mm
G2-1	3.60	49.5	41.3	30.9	26.3	24.8	16.5
G2-2	2.96	40.7	33.9	25.4	21.7	20.4	13.6
G2-3	2.40	33	27.5	20.6	17.6	16.5	11
G2-4	2.00	27.5	22.9	17.2	14.6	13.8	9.2
G2-5	1.68	23.1	19.3	14.4	12.3	11.6	7.7
G2-6	1.44	19.8	16.5	12.4	10.5	9.9	6.6
G2-7	1.28	17.2	14.7	11	9.4	8.8	5.9
G2-8	1.12	15.4	12.8	9.6	8.2	7.7	5.1
G2-9	0.96	13.2	11	8.3	7	6.6	4.4
G2-10	0.80	11	9.2	6.9	5.9	5.5	3.7
G2-11	0.64	8.8	7.3	5.5	4.7	4.4	2.9
G2-12	0.48	6.6	5.5	4.1	3.5	3.3	2.2
G2-13	0.32	4.4	3.7	2.8	2.3	2.2	1.5
G2-14	0.16	2.2	1.8	1.4	1.2	1.1	0.7
S-1	4.80	66	55	41.3	35.1	3 3	22
S-2	4.16	57.2	47.7	35.8	30.4	28.6	21.1
S-3	3.60	49.5	41.3	30.9	26.3	24.8	16.5
S-4	2.96	40.7	33.9	25.4	21.7	20.4	13.6
S-5	2.40	33	27.5	20.6	17.6	16.5	11
S-6	2.00	27.5	22.9	17.2	14.6	13.8	9.2
S-7	1.68	23.1	19.3	14.4	12.3	11.6	7.7
S-8	1.44	19.8	16.5	12.4	10.5	9.9	6.6
S-9	1.28	17.2	14.7	11	9.4	8.8	5.9
S-10	1.12	15.4	12.8	9.6	8.2	7.7	5.1
S-11	0.96	13.2	11	8.3	7	6.6	4.4
S-12	0.80	11	9.2	6.9	5.9	5.5	3.7
S-13	0.64	8.8	7.3	5.5	4.7	4.4	2.9
S-14	0.48	6.6	5.5	4.1	3.5	3.3	2.2
S-15	0.32	4.4	3.7	2.8	2.3	2.2	1.5
S-16	0.16	2.2	1.8	1.4	1.2	1.1	0.7

APPENDIX 2

Size of the 14 stimuli used to measure resolution acuity with the staircase procedure. The sizes are expressed in c/deg based on a viewing distance of 500 mm.

STIMULUS	SIZE (C/DEG)
1	0.44
2	0.87
3	1.25
4	1.45
5	1.75
6	2.04
7	2.33
8	2.63
9	3.03
10	3.64
11	4.48
12	4.85
13	7.27
14	9.70

APPENDIX 3

Size of the 53 stimuli used to measure resolution acuity with the method of limit. The sizes are expressed in c/deg based on a viewing distance of 570 mm.

STIMULUS	SIZE	STIMULUS	SIZE
1	0.28	28	2.08
2	0.33	29	2.22
3	0.37	30	2.27
4	0.40	31	2.38
5	0.46	32	2.56
6	0.49	33	2.63
7	0.56	34	2.78
8	0.65	35	2.82
9	0.67	36	2.94
10	0.74	37	3.13
11	0.80	38	3.23
12	0.89	39	3.33
13	1.02	40	3.45
14	1.11	41	3.57
15	1.16	42	3.70
16	1.28	43	3.85
17	1.35	44	4.0
18	1.39	45	4.17
19	1.45	46	4.44
20	1.48	47	4.76
21	1.54	48	5.0
22	1.59	49	5.26
23	1.67	50	5.71
24	1.72	51	6.25
25	1.79	52	6.67
26	1.89	53	7.69
27	1.93		

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