

Behavioral and Morphological Evidence for Binocular Competition in the Postnatal Development of the Dog's Visual System¹

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ABSTRACT Two normally-reared dogs and five dogs reared with monocular eyelid closure were studied. The two normal dogs and three of the deprived dogs were tested with a perimetry technique for the extent of behavioral visual field, and all of the dogs were studied histologically to determine the size of cell somata in the lateral geniculate nucleus.

Behaviorally, the normal dogs saw with each eye approximately from 120° ipsilateral to 30° contralateral. The deprived dogs had a normal field of view for the non-deprived eye, but with the deprived eye they saw only in the monocular segment (i.e., approximately 120° to 30° ipsilateral).

Histologically, geniculate cells in the monocular segment of deprived dogs were of normal size. In the deprived laminae of the binocular segment, however, cells averaged about two-thirds normal size, and in non-deprived laminae of this segment, neurons were hypertrophied. The hypertrophy was greater for cells in lamina A (40%) than for those in lamina A1 (17%).

These data indicate that in monocularly deprived dogs, the monocular segment of the visual system develops normally, but the binocular segment does not. Therefore, we conclude that binocular competition operates in the developing dog's visual system much as it does in the cat's.

Some form of binocular competition affects the postnatal development of neurons in the cat geniculostriate system (see Sherman et al., '74 for a full discussion of this). Recently Guillery and Kaas ('74a) and Casagrande et al. ('74) have obtained morphological evidence for binocular competition operating in the lateral geniculate nucleus of the squirrel and tree shrew, respectively. In the present account, we provide evidence for binocular competition in the dog's visual system. Not only does this extend the concept of binocular competition to another species, but since we gathered both morphological and behavioral data, this represents the first functional evidence, to our knowledge, of binocular competition in a species other than the cat.

Binocular competition has been demonstrated most convincingly in animals reared with the lids of one eye sutured, a condition which confers a competitive advantage to the central neurons associated with the non-deprived eye. In such a monocularly deprived cat, cells of the lateral geniculate

laminae receiving afferents from the deprived eye are abnormally small (Wiesel and Hubel, '63a; Guillery and Stelzner, '70) and have a severely reduced complement of Y-cells (Sherman et al., '72; Hoffmann and Sherman, '74), whereas the non-deprived laminae are normal. Neurons of the striate cortex, most of which in normal cats are driven by either eye (Hubel and Wiesel, '62), are nearly exclusively driven by the non-deprived eye in the lid-sutured cats (Wiesel and Hubel, '63b; Ganz et al., '68). Finally, such a cat seems nearly blind when forced to use its deprived eye (Ganz and Fitch, '68; Dews and Wiesel, '70; Rizzolatti and Tradardi, '71).

That this results from a form of binocular competition in the geniculostriate system is best indicated by comparing the deprivation results in the *binocular segment* with those in the *monocular segment* (cf. Guillery and Stelzner, '70; Sherman et al., '72; Guillery and Kaas, '74a; Sherman et al., '74). Cells in the binocular segment

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receive their input from the central, binocularly-viewed portion of visual field, while those in the monocular segment receive input from the peripheral, monocularly-viewed crescent. Apparently, monocular deprivation in cats selectively affects the binocular segment whereas the monocular segment, in which binocular competition is logically impossible, develops fairly normally. That is, in the monocular segment of the lateral geniculate, the deprived laminae have cells both of normal size (Guillery and Stelzner, '70) and with the normal Y-cell proportion (Sherman et al., '72). Furthermore, in this segment of cortex, neurons appear to be briskly activated by appropriate visual stimulation of the deprived eye (Sherman et al., '74), and on behavioral testing with this eye, the cat ignores visual stimuli in the binocular segment of visual field but readily orients to them in the monocular segment (Sherman, '73, '74). That this is a true result of binocular competition and not a central/peripheral difference is indicated by data from lid-sutured cats raised with a central, monocular segment which is artificially created by destroying a patch of central retina in the non-deprived eye. In this artificial monocular segment corresponding to the deprived eye, geniculate cells grow normally (Guillery, '72), cortical neurons are clearly responsive to visual stimuli (Sherman et al., '74), and the animal readily orients to visual stimuli (Sherman et al., '74).

Given the developmental mechanism of binocular competition for the cat's geniculostriate system, it is important to know how generally this phenomenon applies to other mammalian species. One simple way to determine this would be to compare the differential effects of monocular deprivation on the binocular and monocular segments in the species of interest (Guillery and Kaas, '74a; Casagrande et al., '74; Sherman et al., '74). We have done this in the dog in a study of geniculate histology and behavioral visual perimetry, and we have found that the deleterious effects of monocular deprivation were limited to the binocular segment. These results have been reported earlier in preliminary form (Sherman and Wilson, '74).

MATERIALS AND METHODS

Seven mongrel dogs were used in this

experiment, and each as adults weighed approximately 20 kg. These were chosen so as to avoid dogs with unusually long or short snouts. Two normal control dogs (N1, N2) were acquired as young adults. The five experimental dogs were born and reared in the laboratory. At eight days of age, before the eyelids opened naturally, these five had the lids of either the right eye (R1, R2, R3) or left eye (L1, L2) sutured together by a previously described method (cf. Wiesel and Hubel, '63a). Dogs R3 and L1 were used solely for histological data and were sacrificed at eight months of age (i.e., young adulthood) never having had their deprived eyes opened. Dogs R1 and R2 had their eyelids opened at six months of age under barbiturate anesthesia, were behaviorally tested during the ensuing two months and were then sacrificed and prepared for histological study. Dog L2 had a reverse-suture operation at seven months of age; i.e., the left eye was opened and the right eye closed. This animal was monocularly tested during the next eight months; then the right eye was reopened for another 2-month's testing; and, finally the animal was sacrificed and prepared for histological study. This last dog allowed an estimate of both the permanence of early deprivation effects and also the possible results of adult deprivation (cf. Dews and Wiesel, '70; Chow and Stewart, '72; Sherman, '74).

Behavioral testing

To study non-learned, visually guided behavior in the dogs, we used behavioral tests which were only slightly modified from those described for the cat (for details, see Sherman '73, '74), and a brief account follows. The dog fixated on one visual stimulus while a second object was vertically introduced into a limited portion of the visual field. The dog's response to this second object (i.e., orientation or lack of orientation to it) determined the functional, horizontal extent of visual field. Every 15° sector was repeatedly tested. An important control consisted of determining the rate of "blank" responses (cf. Sherman, '73, '74). That is, we determined the rate of spontaneous turning in the absence of a second object, since this turning could be mistaken for stimulus-evoked orienting. The only portions of the field considered to be functional for the dog were those in which objects elic-

ited rates of appropriate orienting significantly higher than the blank rate. The dogs were tested with both eyes open and with one or the other eye occluded by means of a small eye patch (unlike cats, the dogs refused to tolerate contact corneal occluders, even with ophthalmic anesthetics). Finally, we attempted to assess both their ability to follow moving targets and also their visual placing responses.

Histological methods

All seven dogs were anesthetized and sacrificed by transcardial perfusion of saline followed by 10% formol-saline. The brains were stereotaxically blocked, embedded in celloidin and cut coronally at 40 μm . Most sections through the lateral geniculate nucleus were stained with cresylecht violet while occasional sections were stained for myelinated fibers. We measured cross-sectional areas of individual geniculate cell bodies by tracing their outlines onto graph paper with a *camera lucida* microscope attachment. Oil-immersion optics at 1,000 \times were used, and the area in square microns was measured by counting the squares inside each outline and converting this by means of a micron scale drawn onto the paper with the same optical system.

For each dog, we measured 150 cells from six geniculate areas of 25 cells each (3 areas from each geniculate — from laminae A and A1 in the binocular segment and from the monocular segment of lamina A). The following precautions were taken to minimize sampling errors. Matched geniculate areas were studied by choosing the same antero-posterior level. We accomplished this by noting the sections which included the rostral and caudal poles of the geniculate, by selecting sections at the same antero-posterior level in the anterior half, and by choosing matched medio-lateral zones in these sections (fig. 4). Only neurons with clearly visible nucleoli were measured. Finally, our graph paper had concentric circles drawn on it, and we selected for study only the 25 neurons closest to the center of these circles. Often these 25 neurons had to be initially identified at 400 \times magnification.

RESULTS

Behavioral testing

The two normal dogs, N1 and N2, plus

deprived dogs R1, R2, and L2 were behaviorally studied. They generally provided clear data on the tests we applied, although they did not respond quite as briskly or consistently as did cats on a similar battery of tests (cf. Sherman, '73 for details). We failed to demonstrate consistent visual placing or following in any of the dogs, so the account below deals solely with the perimetry data.

Normal perimetry

Figure 1 summarizes the perimetry data for dogs N1 and N2. With binocular viewing, each dog had a 240 $^\circ$ field of view, extending to 120 $^\circ$ on either side (fig. 1A). These lateral boundaries seemed quite sharp as we consistently elicited orientation by placing objects at 120 $^\circ$ to either side and just as consistently failed to elicit such behavior with the objects at 130 $^\circ$. With monocular viewing (fig. 1B,C) the dogs see from 120 $^\circ$ ipsilateral to the open eye to 15 $^\circ$ or 30 $^\circ$ across the midline. Again, the ipsilateral boundary appeared to be sharp, but the contralateral boundary seemed relatively vague and variable. The fact that the ipsilateral boundary remained crisp suggests that the inconsistency seen in the contralateral boundary was not due to inconsistent visual fixation by the dogs.

In summary, these data place the dog's binocular segment of visual field within the boundaries of 15–30 $^\circ$ on either side of the midline. The monocular segments on either side extend from 120 $^\circ$ to about 30 $^\circ$ or 15 $^\circ$. Finally, the differences in boundaries between dogs (i.e., note the different response levels at 30 $^\circ$ right for N1 and N2 in fig. 1B) raise the possibility of individual variability in the boundaries between binocular and monocular segments.

Perimetry of deprived dogs

Dogs R1 and R2. We began testing dogs R1 and R2 several weeks after the right eyes were opened, and the data are summarized by figure 2. As in the normal dogs, slight individual differences were seen. For instance, figure 2A shows that dog R1 had a normal binocular field of view extending 120 $^\circ$ to either side while dog R2 had a binocular field from 120 $^\circ$ left to only 105 $^\circ$ right. The fields of the non-deprived eye in figure 2B were also slightly different: for dog R1 it extended from 120 $^\circ$ left to 45 $^\circ$

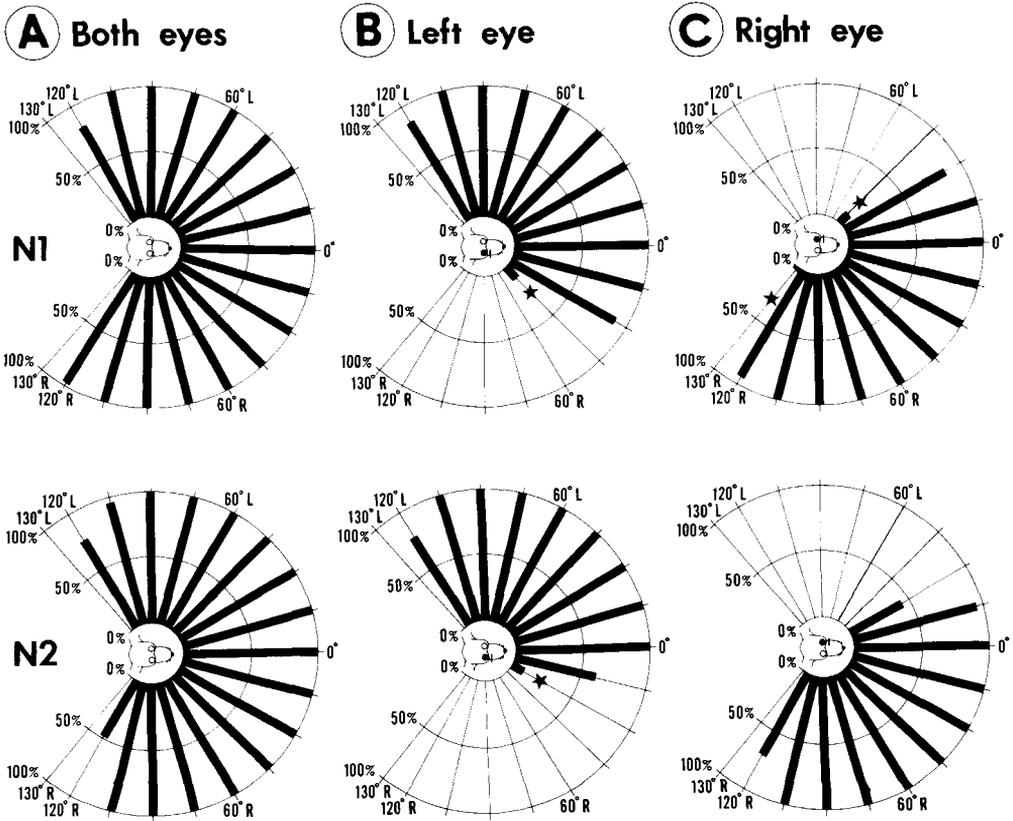


Fig. 1 Behavioral visual fields for the normally-reared dogs. The positive response levels for each visual field sector are shown as black bars. These levels are normalized against a background of blank positive responses (MATERIALS AND METHODS) which are less than 20% for all charts in this and succeeding figures. Every guideline was tested repeatedly. The bars indicated by a star represent levels not significantly higher than blank levels ($p > 0.05$ on a χ^2 -test). All other bars represent levels which are significantly higher than the blank levels ($P < 0.001$ on a χ^2 -test). A: Binocular field. B: Field for the left eye. C: Field for the right eye.

right; for dog R2, from 120° left to 30° right.

From this and considerations of the perimetry of dogs N1 and N2 it follows that the monocular segment for the deprived eye can be defined as follows: it is the difference between the field of view seen by both eyes and that seen by the non-deprived eye (i.e., the fields of fig. 2A minus those of fig. 2B; see also Sherman, '73). Given this definition of the deprived eye's monocular segment, figure 2C shows that this region, and essentially only this region, was attended to by that eye.

Two further details are worth noting. First, dog R2 appeared to see further to the right with the right eye alone than with

both eyes (i.e., note the response levels at 120° right in fig. 2A,C). Such a discrepancy was seen in no other dog, nor was it seen in any cat previously tested (Sherman, '73, '74). We cannot explain this discrepancy except to suggest that such factors as strabismus and eccentric fixation (Sherman, '72, '73) could cause the right eye's visual axis to align differently in binocular vs. monocular viewing. Second, dog R1 responded to objects at 45° right with either eye, thereby implying that the deprived eye saw into the binocular segment. However, these response levels at 45° right were both much reduced from those at the neighboring portions (i.e., 30° right for the left eye, 60° right for the right eye), and this

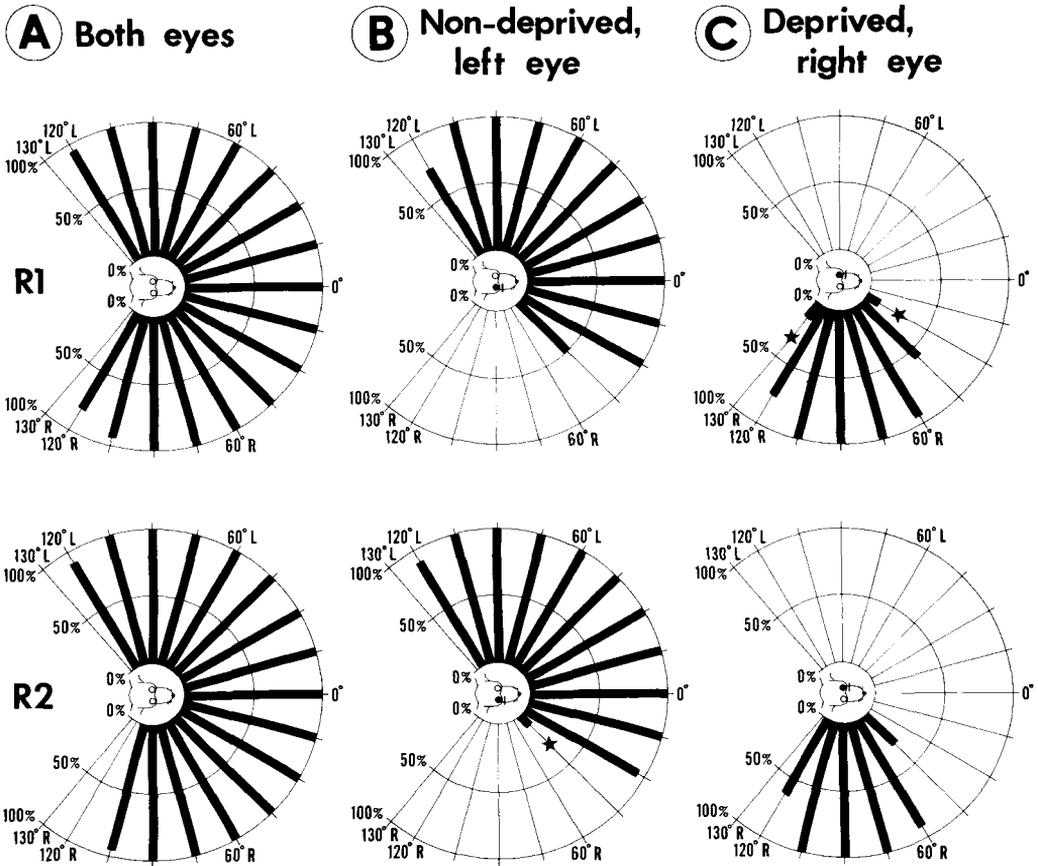


Fig. 2 Behavioral visual fields for visually deprived dogs R1 and R2; conventions as in figure 1. A: Binocular field. B: Field for the non-deprived, left eye. C: Field for the deprived, right eye.

suggests that for dog R1 the boundary between binocular and monocular segments passes very near to 45° right. Thus, we could have sometimes been stimulating binocular segment, and other times, monocular segment, during tests at 45° right. In fact the boundary between segments may be oblique or curved (as it is in man) and pass through 45° so that our vertical presentation of the stimulus would at some positions be in binocular segment and at others, in monocular segment.

Dog L2. This dog was tested first with the normal right eye before the reverse-suture operation, and the field seemed normal. Figure 3A shows the right eye's field after this eye had been shut for many months, and the field still appeared normal and totally unaffected by the adult period

of deprivation. The field extended from 120° right to 45° left.

During final testing of the left (originally deprived) eye, this dog's perimetry responses were by far the vaguest of any. In this condition the dog's fixation and apparent field of view seemed variable from day to day, and we cannot explain this inconsistency. The field summary in figure 3B is thus subject to error. Nonetheless, with this eye the dog behaved much more like dogs R1 and R2 when they used only the deprived eye than any of the dogs using the normal or non-deprived eye. That is, the extensive and exclusive adult experience with the originally deprived eye did not substantially improve its field of view. It remains unclear whether or not the responses at 45° and 30° right imply vision into the

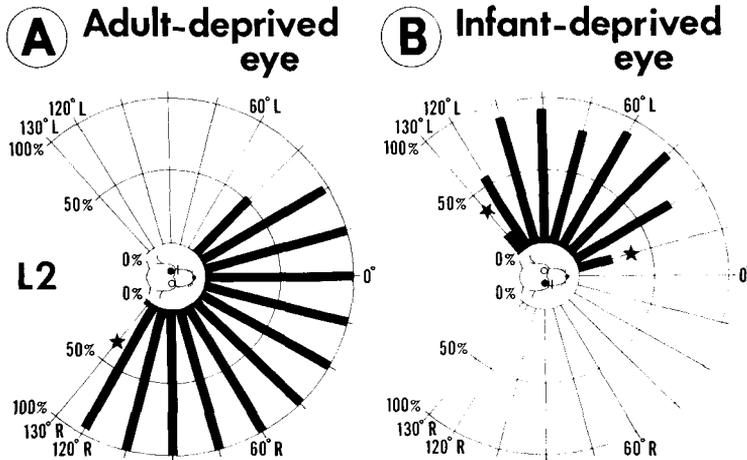


Fig. 3 Behavioral visual fields for the reverse-sutured dog, L2: conventions as in figure 1. A: Field for the adult-deprived eye (see text). B: Field for the infant-deprived eye.

binocular segment, which, in turn, could constitute behavioral recovery. This would be in contrast to the total lack of such recovery in the cat (Sherman, '74). On the other hand, these responses in the binocular segment could have been due to artifacts such as those described above for dogs R1 and R2, artifacts which were compounded by this dog's singularly inconsistent performance. Clearly further data with a more reliable test are necessary to answer this question completely, but we tentatively conclude that any behavioral recovery in dog L2 is minimal if it occurs at all.

Histological studies

Lateral geniculate. The dorsal lateral geniculate nucleus in the dog is laminated in a fashion similar to that for the cat (Rioch, '29; Kaas et al., '72). This paper is concerned primarily with the dorsal two laminae which, because of this similarity to the cat geniculate, are called A and A1 (fig. 4). We assume that, in the dog, lamina A receives afferents from the contralateral eye and lamina A1, from the ipsilateral eye, since this is the pattern seen in the cat and other carnivores (Kaas et al., '72). This assumption is supported by the histological data presented below.

As in the cat, it was immediately clear that the deprived laminae in the dog geniculate had abnormally small cells when compared to cells in the non-deprived laminae (fig. 4). We measured 150 cells from each

of the five deprived dog's geniculates. These were in groups of 25 each from the following six carefully matched areas: (1) and (2) binocular segment of deprived and non-deprived lamina A, (3) and (4) deprived and non-deprived lamina A1, (5) and (6) monocular segment of deprived and non-deprived lamina A. From each of the normal dogs we measured 25 cells each from the binocular segment of lamina A, lamina A1 and the monocular segment of lamina A (MATERIALS AND METHODS and also figs. 4, 5). This was done unilaterally in dog N2 (N = 75) and bilaterally in dog N1 (N = 150) so that we measured a total of 225 cells in the normal dogs.

Table 1 summarizes these data for all of the dogs. Three key points emerge: (1) in the binocular segment, cells in the deprived laminae are significantly smaller on the average than either normal cells or cells in non-deprived laminae; (2) in the monocular segment of lamina A, deprived cells, non-deprived cells, and cells in the normal dog are of essentially equal size; and (3) dog L2 has the same pattern of geniculate cell size as would be expected without the adult reverse-suture operation.

The second point above implies that, as in the cat (Guillery and Stelzner, '70), geniculate cell sizes in the dog's monocular segment are unaffected by monocular deprivation. Assuming this to be the case, we can make more detailed comparisons between dogs by normalizing all cell sizes

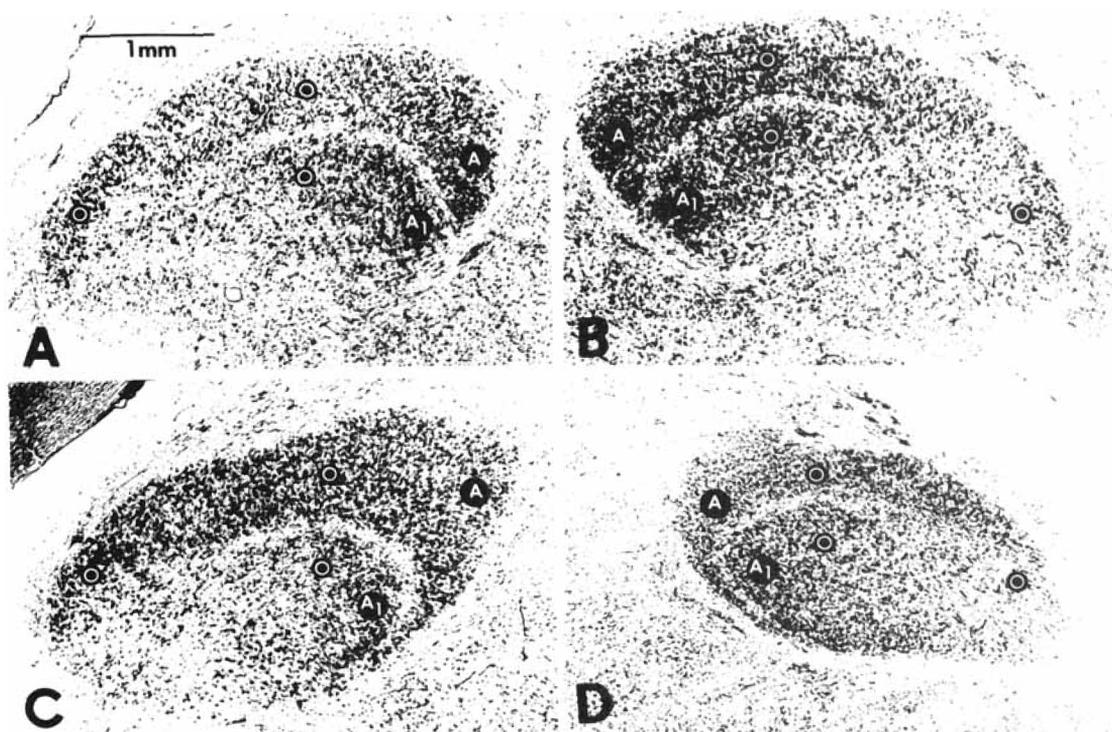


Fig. 4 Photomicrographs of the lateral geniculates of a normal dog, N2, and a visually deprived dog, L1. The sections are those from which cell measurements were made (see text). The concentric circles represent the approximate zones of these measured cells in the binocular segment of laminae A and A1 plus the monocular segment. A: Left geniculate of dog N2. The scale is the same for B-D. B: Right geniculate of dog N2. C: Left geniculate of dog L1; lamina A receives terminals from the non-deprived eye; lamina A1, from the deprived eye. D: Right geniculate of dog L1; lamina A receives terminals from the deprived eye; lamina A1, from the non-deprived eye.

TABLE 1

Dog	Left geniculate			Right geniculate		
	A ¹	A1 ¹	Monoc. seg.	A ¹	A1 ¹	Monoc. seg.
N1	214 ± 17	230 ± 23	245 ± 24	216 ± 17	229 ± 22	227 ± 15
N2	196 ± 15	204 ± 20	249 ± 19			
	Geniculate contralateral to deprived eye			Geniculate ipsilateral to deprived eye		
	A ¹	A1 ¹	Monoc. seg.	A ¹	A1 ¹	Monoc. seg.
R1	119 ± 11	208 ± 14	217 ± 14	240 ± 22	134 ± 26	240 ± 17
R2	111 ± 8	220 ± 15	216 ± 14	232 ± 17	153 ± 14	212 ± 19
R3	135 ± 17	274 ± 29	218 ± 15	273 ± 17	151 ± 20	212 ± 14
L1	75 ± 4	165 ± 13	141 ± 8	217 ± 16	91 ± 10	168 ± 10
L2 ²	119 ± 9	244 ± 19	213 ± 14	277 ± 23	125 ± 10	219 ± 10

Cell sizes in μm^2 . Each sample represents the mean \pm one standard error for 25 cells.

¹ Denotes binocular segment.

² Reverse-sutured dog (see text).

with respect to those in the monocular segment of dogs N1 and N2, and this has been done in figures 5, 6. This obviates differences in cell sizes caused by uncontrolled variables in tissue processing.² For instance, these cells average $240 \mu\text{m}^2$ in dogs N1 and N2 and $228 \mu\text{m}^2$ in dog R1, so we have multiplied all cell sizes in dog R1 by the fraction 240/228. This type of normalization was carried out in turn for each of the other dogs.

Figure 5 summarizes these normalized data of average cell size for each of the dogs. Seen in this fashion, there is little difference between dogs in terms of deprivation effects on geniculate histology. This further substantiates the conclusion that the reverse-suture procedure in dog L2 had no further effect on geniculate histology. The last histogram in figure 5, by showing the combined data for the five deprived and the two normal dogs, summarizes the essential histological details: (1) In the normal dog, lamina A1 cells tend to be larger than those of lamina A (but his difference is not significant since $p > 0.05$ on a t-Test), and in lamina A, cells of the monocular segment tend to be larger than those of the binocular segment ($p < 0.01$ on a t-Test). (2) Cells in both deprived laminae, A and A1, are abnormally small ($p < 0.001$ on a t-Test) by approximately the same amount (38% and 31% smaller than normal, respectively). (3) Cells in both non-deprived laminae, A and A1, are larger than normal ($p < 0.001$ on a t-Test for both comparisons), but the 40% hypertrophy for lamina A neurons significantly exceeds the 17% hypertrophy for lamina A1 neurons ($p < 0.001$ on a t-Test). (4) The result of the last two points above is that, for lamina A, the size of the deprived cells averages only 45% of that of the non-deprived neurons, and for lamina A1, the proportion is 59%.

Finally, figure 6 shows the frequency histogram of different cell sizes for geniculate laminae in the normal and deprived dogs. These cell sizes have been normalized as described above. From these histograms, it is clear that the largest cells are affected by deprivation; whether or not the smaller cells are also affected cannot be determined from our present data.

Cortex. Guillery and Kaas ('74b) reported obvious interhemispheric differences in

the appearance of striate cortex in monocularly deprived squirrels. Cortex contralateral to the deprived eye was thinner and had more tightly packed cells than ipsilateral cortex; this asymmetry occurred in both monocular and binocular segments. Such an asymmetry has not been reported for cats. We found no such interhemispheric differences in the appearance of cortex in any of the monocularly deprived dogs, although we emphasize that careful measurements were not made.

DISCUSSION

Data from both visual perimetry testing and geniculate histology indicate that monocularly deprived dogs develop visually by means of some form of binocular competition. That is, whereas the visual field for the non-deprived eye was normal, that for the deprived eye was limited to the monocular segment. Furthermore, cells receiving retinal afferents from the deprived eye were abnormally small in the binocular segment of the geniculate but were of normal size in the monocular segment. These effects of early deprivation are in no way alleviated by adult experience exclusively through the previously deprived eye, nor does adult deprivation seem to deleteriously affect central connections from an eye which had been used during development. In practically every detail, these effects of deprivation in the dog closely parallel similar phenomena in the monocularly deprived cat (cf. Sherman, '73, '74; Guillery and Stelzner, '70).

Visual perimetry

Figure 7 illustrates that the normal dog has a larger binocular field of view than the cat, 240° versus 180° . This is because the cat, when compared to the dog, has both more binocular overlap (approximately, 90° compared to 60°) and a smaller monocular field for either eye (approximately, 135° compared to 155°). Given these quantitative differences, the behavior on the perimetry test was remarkably similar for cats and dogs, and monocular deprivation created the same qualitative visual field deficit (fig. 7).

² Table 1 shows that the geniculate cells from dog L1 are the smallest of any in the study. This is probably an artifact due to differential tissue shrinkage during histological processing, since all of the thalamic nuclei seemed smallest for this dog (also Guillery, '73).

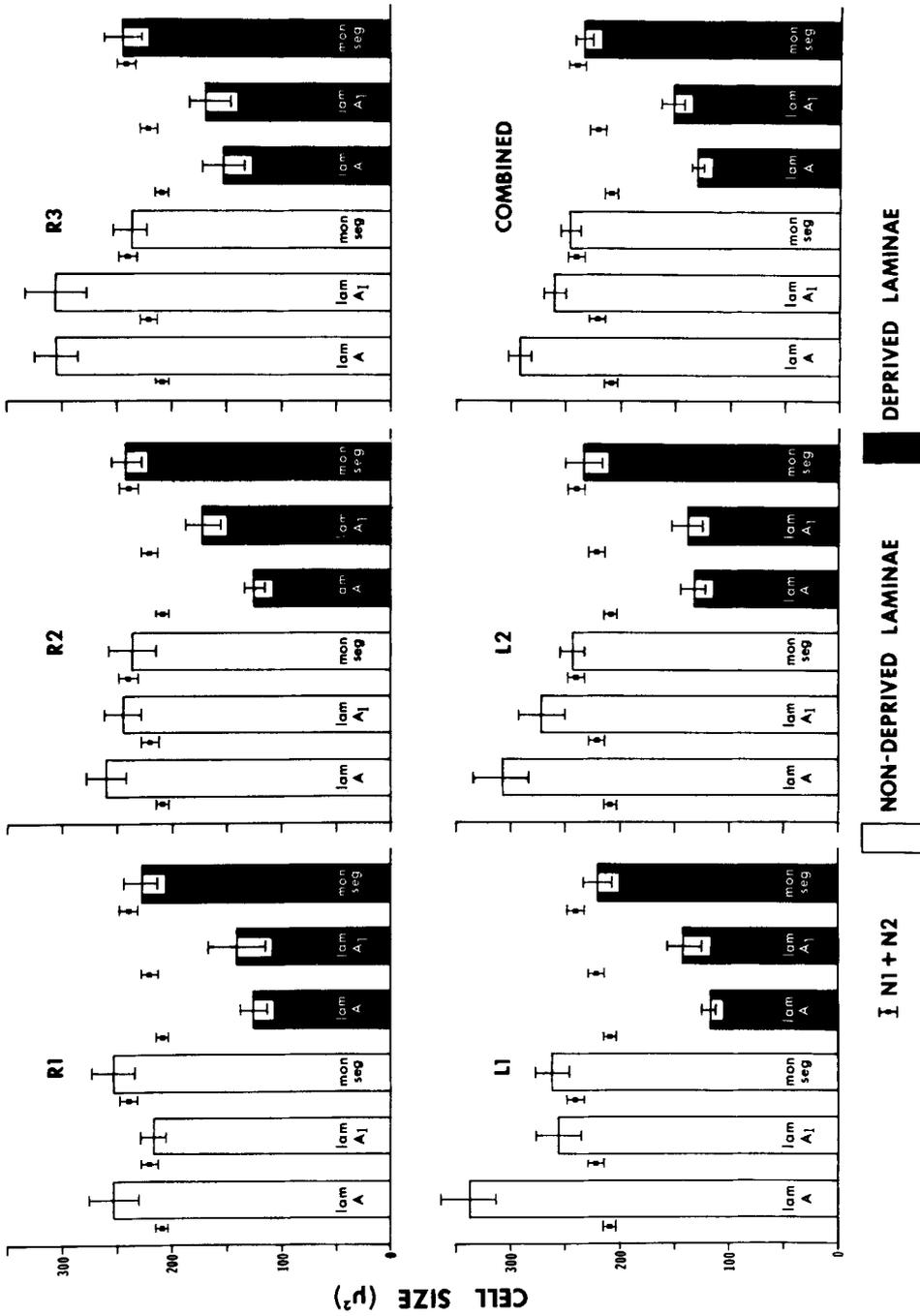


Fig. 5 Histograms of average geniculate cell sizes (\pm one standard error) in each sector measured. All sizes have been normalized with respect to sizes in the monocular segment (see text). For comparison, each chart includes for each sector the average cell sizes (\pm one standard error) of dogs N1 and N2. In the deprived dogs, non-deprived laminae are those which receive direct retinal afferents from the non-deprived eye; deprived laminae, from the deprived eye.

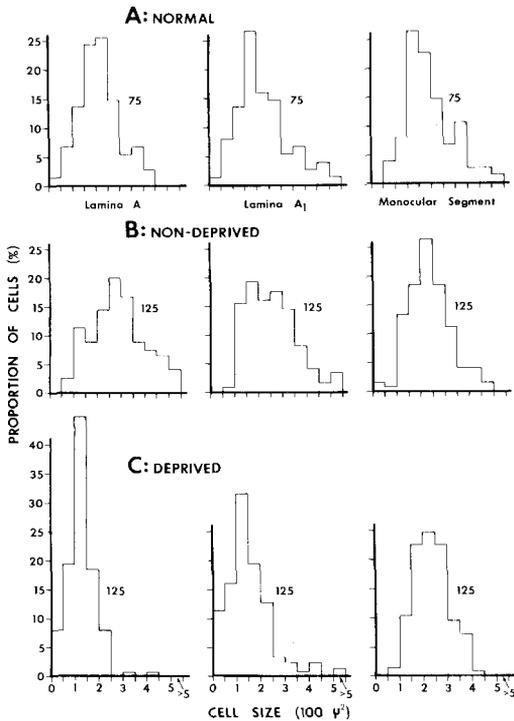


Fig. 6 Histograms showing the relative frequency of cells of various sizes. All sizes were normalized before plotting with respect to sizes in the monocular segment (see text). The total number of cells counted for each histogram is indicated. See legend of figure 5 for definition of non-deprived and deprived laminae. A: Relative frequency of cell sizes for the normal dogs (N1 and N2). B: Relative frequency of cell sizes for non-deprived laminae in visually deprived dogs (R1, R2, R3, L1, L2). C: Relative frequency of cell sizes for deprived laminae in visually deprived dogs (R1, R2, R3, L1, L2).

The only previous estimates for the dog's visual field known to us resulted from optical considerations. Walls ('42), for instance, estimated the dog's binocular field of view to be 250° , and this closely matches our behavioral estimate. However, Walls also suggested that the dog's binocular overlap varies, depending on species, from $78^\circ 40'$ to $116^\circ 20'$. These values are larger than our behavioral estimates, perhaps because the snout blocks more of the field seen by temporal retina than was anticipated.

Histology

Geniculate. In deprived geniculate laminae, both the abnormally small size of cells

in the binocular segment and the normal cell size in the monocular segment are most simply explained on the basis of a mechanism involving binocular competition which controls cell growth. This has been previously discussed in detail for cats (Guillery and Stelzner, '70; Guillery, '72; Sherman et al., '74) and need not be further considered here. It is interesting to note that the relative changes in geniculate histology were remarkably consistent among the deprived dogs (fig. 5).

Two other histological features in the deprived dog geniculates were unexpected and merit discussion. First, non-deprived neurons in the binocular segment appeared to hypertrophy. From considerations of binocular competition, Guillery ('72) anticipated this for the cat and stated that preliminary results suggested hypertrophy at least for non-deprived lamina A cells, and in the dog, non-deprived lamina A neurons showed more hypertrophy than those of lamina A1. Whatever factors caused the deprived neurons to be abnormally small could conceivably encourage hypertrophy in the non-deprived neurons. For one example, deprived geniculate neurons might grow less because they fail to make synaptic connections in cortex; the reduced metabolic demands of fewer synapses result in smaller somata. On the other hand, the non-deprived neurons might develop extra synapses at the expense of those lost to the deprived cells, and they would consequently hypertrophy.

The second unexpected result is related to the above hypertrophy. While no obvious interlaminar differences appeared for deprived laminae, lamina A neurons hypertrophied more than those in lamina A1 (see last histogram in fig. 5). This indicates an interhemispheric difference in the deprivation effects within the binocular segment such that geniculate neurons contralateral to the deprived eye are, on the average, smaller than those ipsilateral to this eye. For instance, notice from the last chart of figure 5 that the average cell size in the deprived lamina A plus the non-deprived lamina A1 (i.e., contralateral to the deprived eye) is smaller than the average in the non-deprived lamina A plus the deprived lamina A1 (i.e., ipsilateral to the deprived eye).

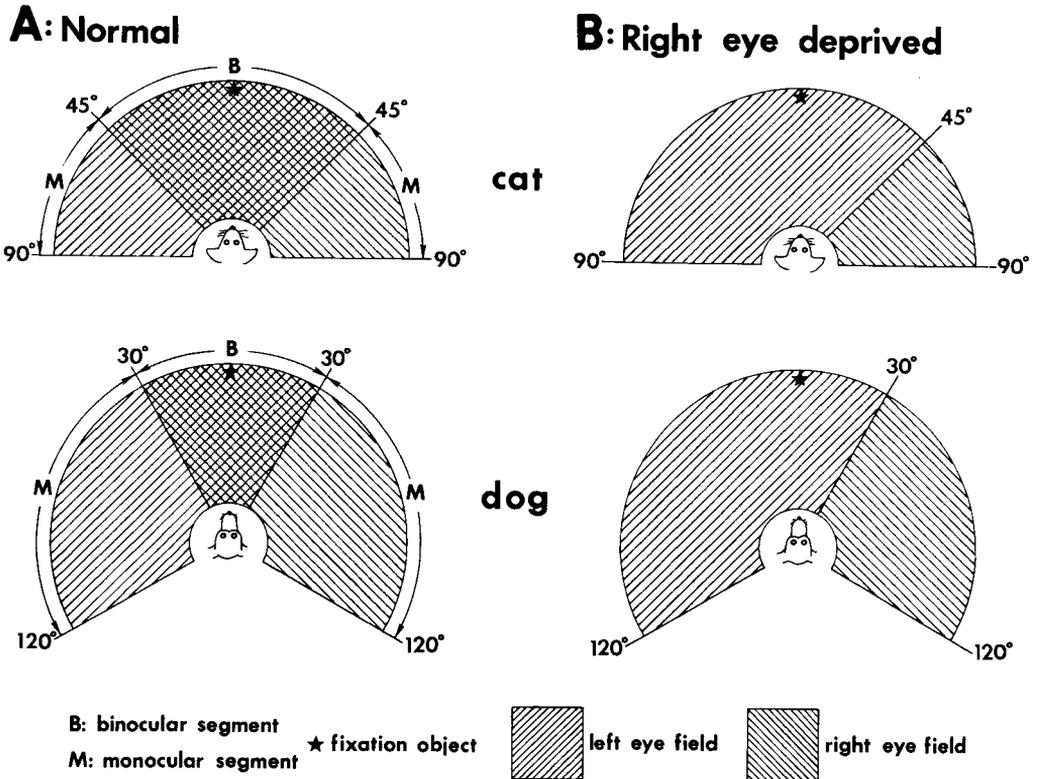


Fig. 7 Idealized comparison of behavioral visual fields for dogs and cats, both normal and monocularly deprived. In all cases, the binocular field equals the combined extent of the two monocular fields. A: Fields for normal cats and dogs. Compared to the cat, the dog has a larger overall field, with a larger monocular segment but smaller binocular segment. B: Fields for (right) monocularly deprived cats and dogs. In both cases, the non-deprived eye has a normal field of view, but the deprived eye sees only in its monocular segment.

Critical period

The existence of a "critical period" in visual development suggests that only for a limited postnatal period does the environment affect the neurological status of the visual system. That is, adult deprivation does not create new abnormalities, nor does a normal adult environment significantly rectify previously established deprivation deficits. Such a critical period has already been demonstrated for the cat in terms of deprivation effects on cortical physiology (Wiesel and Hubel, '65; Hubel and Wiesel, '70), visual perimetry (Sherman, '74), and geniculate histology and physiology (Wiesel and Hubel, '65; Sherman and Wilson, '75). These data should be interpreted cautiously since other studies of reverse-sutured cats have suggested limited recovery of

discrimination learning by the deprived eye (Dews and Wiesel, '70; Chow and Stewart, '72; Ganz and Haffner, '74) and a dramatic reversal of histological effects in the geniculate (Chow and Stewart, '72). In any case, our present data from dog L2 support the contention of an early critical period since: (1) the behavioral and histological deficits associated with the infant-deprived eye were not substantially changed by an extensive adult period of exclusive use of that eye, and (2) no deficits were found associated with the adult-deprived eye.

Conclusions

Substantial data support the theory of some form of binocular competition in the postnatal development of the cat's visual system (cf. Sherman et al., '74). Recently,

histological studies extended this theory to include the squirrel (Guillery and Kaas, '74a) and the tree shrew (Casagrande et al., '74). We now add the dog to the list of mammalian species in which binocular competition affects visual development, and we support this with both histological and behavioral data.

Cats, squirrels, tree shrews, and dogs apparently share the attribute of fairly extensive binocular vision. To examine more fully the universality of binocular competition as a developmental mechanism, analogous studies comparing the binocular and monocular segments should be performed both on animals with relatively poor binocular vision, such as rabbits (cf. Chow and Spear, '74; Van Sluyters and Stewart, '74), and on animals with even more extensive binocular vision, such as the fovea-dominated primates. Headon and Powell ('73) recently reported that the geniculate of monocularly deprived monkeys has deprived neurons which are smaller than the non-deprived neurons. However, this is not in itself a rigorous demonstration of binocular competition since no attempt was made to identify potentially different deprivation effects in the binocular and monocular segments (cf. discussion in Sherman et al., '74).

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LITERATURE CITED

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