the population oscillation is much longer than that of any individual in the population. The period of these oscillations is a function of the size of the population and strong inhibitory coupling among the individuals of the population. The organization of the population of oscillators in the *Aplysia* eye is probably more complicated than the model by Pavlidis since both excitatory and inhibitory interactions occur in the eye (*8*). If we assume that the interaction between neurons (coupling) remains constant after the eye is cut, then the changes in circadian period and range must be due to the reduction in the number of interacting neurons in the population.

There are at least three alternative models for the organization of the endogenously active neuron (oscillator) population of the eye: (i) a population driven by a master circadian oscillator, (ii) a population of circadian oscillators, and (iii) a population of noncircadian oscillators that together produce a circadian rhythm. If a hypothetical master oscillator does not receive feedback from its followers, the circadian period should stay constant at 27.5 hours until the master oscillator is cut away. Since this does not happen, we assume that if a master oscillator is present it receives feedback from its followers and thus population interactions occur. A master oscillator does not seem to be present, since slightly below the critical level a circadian remnant is still observed, as in Fig. 4, but it is not observed in the minimal eye (0.02 of the population). If the eye is a population of circadian oscillators, the minimum population should show circadian oscillations at least in the first free-running period because each oscillator's phase should still be influenced by the previous light-dark cycle and a circadian rhythm should be observed. Minimal (0.02) eyes express only ultradian frequencies, so this model does not seem to fit. The last alternative of a population of noncircadian oscillators is the most likely because the circadian range and period shorten in proportion to the remaining population until the critical level is reached; below that level a circadian remnant is expressed, and finally only shorter ultradian frequencies appear. The higher order interactions that produce the circadian rhythm are lacking when the population is reduced below the critical level.

Pavlidis (*3*) has suggested that systems of coupled oscillators may be responsible for circadian periodicities at biochemical levels in single cells as well as in populations of interacting cells. The eye of *Aplysia* is an example of a population of interacting neuronal oscillators that produces circadian periodicities.

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## Anomalous Retinal Pathways in the Siamese Cat: An Inadequate Substrate for Normal Binocular Vision

Abstract. *All major retinal pathways in the Siamese cat are abnormal, with almost total crossing of the projections to the pretectum and superior colliculus. These projections represent a marked disruption in the customary neural substrate for binocular vision, which implies a consequent impairment in stereoscopic depth perception. Crossed eyes, commonly seen in the Siamese cat, may therefore arise from a neuroanatomical defect in the primary visual pathways.*

Crossed eyes and squint have been associated with improper control of the eye muscles and have therefore been considered to be a deficit in the oculomotor system (*1*). If the ability to utilize binocular information about distance is lost, then the vergence mechanisms coordinating symmetrical eye movements would be disrupted, for there would be inadequate sensory input to guide the oculomotor system (*2*). Because of the high incidence of crossed eyes in the Siamese cat, we investigated the primary visual pathways in this animal. Guillery found abnormalities in one of the three pathways from the retina (*3*). We show that all of the major retinal pathways of the Siamese cat are abnormal.

In the normal, ordinary cat, the retinal ganglion cells send their axons bilaterally to three major visual centers: the dorsal lateral geniculate nucleus of the thalamus, the pretectum, and the superior colliculus (*4–6*). Axons from the nasal retina of each eye cross to the opposite side of the brain and make their connections contralaterally, whereas axons from the temporal retina remain almost exclusively uncrossed and terminate ipsilaterally, for the most part (*6–8*). As a result of this partial crossing of optic nerve fibers, each subcortical visual center receives binocular information about the contralateral visual field, because the nasal retina of one eye views the same visual field as the temporal retina of the other. It is the precise organization of the visual pathways that most probably forms the substrate for normal binocular vision. If a portion of the input from one eye were disarranged or missing, binocular integration in the visual pathway would be disrupted. The retinal projections of the Siamese cat form an anatomical system which is disorganized, and which is consequently an inadequate substrate for normal binocular integration.

Three adult (unrelated) Siamese cats and one 6-week-old kitten were used in these experiments. In each animal the right eye was enucleated aseptically under deep anesthesia. Five to eight days after the operation, the animals were again anesthetized and perfused through the heart with 0.9 percent saline followed by 10 percent formaline-saline. Frozen sections of the brain were cut coronally at 30 $\mu$m; every fifth section was stained for degenerating axons and their terminals

by the Fink-Heimer silver method (method 1) (*9*). Adjacent sections were stained with cresyl violet to reveal the organization of cell bodies. Because the results were essentially the same for all of the animals, representative findings from only one Siamese cat will be discussed and contrasted with the normal retinal projections of the ordinary cat.

In a coronal section through the middle third of the dorsal lateral geniculate nucleus of the ordinary cat, the neurons of the nucleus are grouped in three major cell laminae (Fig. 1a). The laminae are separated from each other by an intervening, relatively cell-free fiber plexus. This trilaminated organization is functionally significant because each layer of cells receives input from only one eye. The upper and lower laminae, *A* and *B*, respectively, relay visual information from the nasal retina of the contralateral eye, whereas the middle lamina *A1* receives its input from the temporal retina of the ipsilateral eye (*5*, *6*, *8*, *10*, *11*). Adjacent to the medial border of the dorsal lateral geniculate is a distinct group of cells, the medial interlaminar nucleus. Although these cells are closely associated with the dorsal lateral geniculate, they receive a separate, retinotopically organized input from the ipsilateral and contralateral eye (*12*).

In a coronal section through the dorsal lateral geniculate nucleus of the Siamese cat, the laminar organization of the nucleus is abnormal (Fig. 1b). The fiber plexus that normally delimits a sharp boundary between layers *A* and *A1* is malformed, and consequently, the geniculate cells that would normally receive input from the ipsilateral eye have lost their laminar organization. Instead, lamina *A1* is broken into isolated clusters of neurons, three of which stand out distinctly in most of the coronal sections. One cluster lies near the medial border of the nucleus, another is situated laterally, and a third is located between the medial and lateral cell clusters and somewhat dorsal to them. In contrast to the lateral geniculate, the cellular organization of the medial interlaminar nucleus does not appear to be abnormal.

In view of the fact that the lateral geniculate nucleus of the Siamese cat lacks a clear trilaminated organization, it is not surprising that the pattern of degenerating retinogeniculate fibers is very different from that seen in the normal animal. The ipsilateral retinal projection in the Siamese cat terminates almost exclusively on the neurons of the medial and lateral cell clusters, which are vestiges of the normal lamina *A1* (Fig. 2). Although these two patches of degeneration are present in each of the brains we have examined, the areas of the patches are not constant from animal to animal, which indicates that the total volume of the ipsilateral retinogeniculate projections is variable (*11*, *13*).

Contralateral to the enucleation, dense pericellular degeneration fills most of the lateral geniculate except for those sites that receive ipsilateral connections from the intact eye. Of particular interest is the abnormal region of contralateral degeneration that lies between the two sites which are the remnants of normal lamina *A1*. The cells that receive this abnormal contralateral input are the neurons of the dorsal cluster, which are separated from their neighbors by the abnormally developed fiber plexus that surrounds them (Fig. 1b). Some importance may be attached to this isolation of the dorsal cell cluster in view of the significance of the customary isolation of laminae in the normal lateral geniculate. Laminar isolation in the geniculate provides a functional separation of retinal input (that is, adjacent geniculate laminae receive input from different eyes). Therefore, the similar isolation of the dorsal cell cluster that is seen in the lateral geniculate of the Siamese cat also is likely associated with a functional separation of retinal input; namely, that the cells of the dorsal cluster receive a retinal projection of a distinct origin, which is different not only from the contralateral input to laminae *A* and *B*, but also from the ipsilateral input to the adjacent medial and lateral cell clusters. Anatomical and physiological studies in the Siamese cat by Guillery and Kaas have demonstrated that the contralateral projection to the dorsal cluster neurons arises from temporal, rather than nasal retina (*14*).

Thus, in each dorsal lateral geniculate nucleus the number of connections made with the contralateral eye is greatly increased, as compared with those of the ordinary cat, to the degree

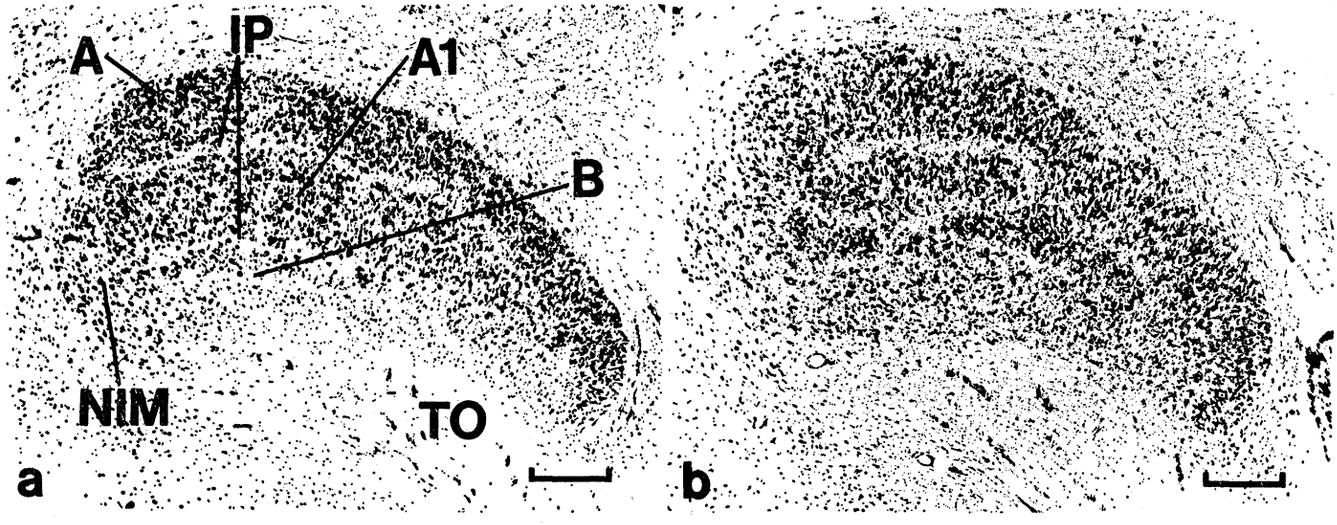


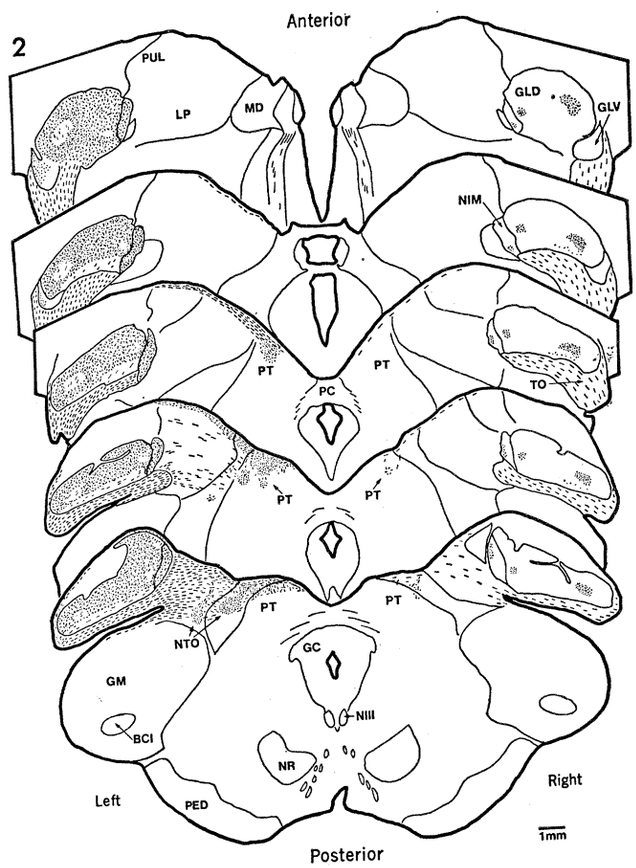

Fig. 1. (a) Coronal section through the middle third of the dorsal lateral geniculate nucleus of any ordinary cat. Cresyl violet stain. *A*, *A1*, and *B* indicate cell laminae; *IP*, interlaminar fiber plexus; *NIM*, medial interlaminar nucleus; *TO*, optic tract. Scale is 0.5 mm. (b) Coronal section through the middle third of the dorsal lateral geniculate nucleus of a Siamese cat. Cresyl violet stain. Note absence of lamina *A1*; instead, from left to right, the medial, dorsal, and lateral cell clusters can be seen. Scale is 0.5 mm.

that the contralateral retinal projections in the Siamese cat occupy much of the space usually reserved for axon terminals from the ipsilateral eye. A similar distribution of crossed as compared to uncrossed optic fibers characterizes the projection of the retina to the medial interlaminar nucleus. Ipsilaterally only a small zone of degeneration is present, whereas in the contralateral nucleus, degenerating fibers can be found throughout most of its extent (*15*). These results are in good agreement with those of Guillery (*3*).

Medial and somewhat posterior to the lateral geniculate nucleus many degenerating axons can be followed into the pretectum where extensive synaptic contacts are made (Fig. 2). In the ordinary cat, the normal projection includes a bilateral distribution of retinal axons to the pretectum; approximately 65 percent cross in the optic chiasm and terminate in the contralateral pretectum, whereas the remaining 35 percent synapse ipsilaterally (*6*). In the pretectum of the Siamese cat on the side of the brain contralateral to the enucleation, the pattern of degenerating axons and terminals appears to be normal. Preterminal degeneration is especially dense in the nucleus of the optic tract that forms the dorsal lateral boundary of the pretectal region, and is its most prominent subdivision. In contrast, however, the ipsilateral pretectum is almost free of degeneration products. Although a few degenerating fibers are visible they are usually scattered and lack the coherent organization that marks a significant axonal pathway. Evidence for terminal degeneration is weak, although it is possible that a small number of synaptic contacts are made in the ipsilateral nucleus of the optic tract.

Posteriorly the pretectum merges with the lateral margin of the superior colliculus (Fig. 3). Retinal fibers enter the colliculus by way of its optic layer (*SO*), and the majority of fibers then turn dorsally to terminate in the superficial grey layer (*SGS*). In the normal cat each colliculus receives a strong projection from the nasal retina of the contralateral eye and a weak, but definite, overlapping projection from the temporal retina of the ipsilateral eye. In the Siamese cat the contralateral retinocollicular projection is well developed, but the ipsilateral projection is almost absent. Only toward the caudal pole of the colliculus where the ipsilateral representation of the peripheral visual field is usually found, is there evidence for a sparse retinal projection.

Our findings in the Siamese kitten suggest that all of the above abnormalities are present at birth, which implies a genetic error. A congenital, rather than acquired defect arising from



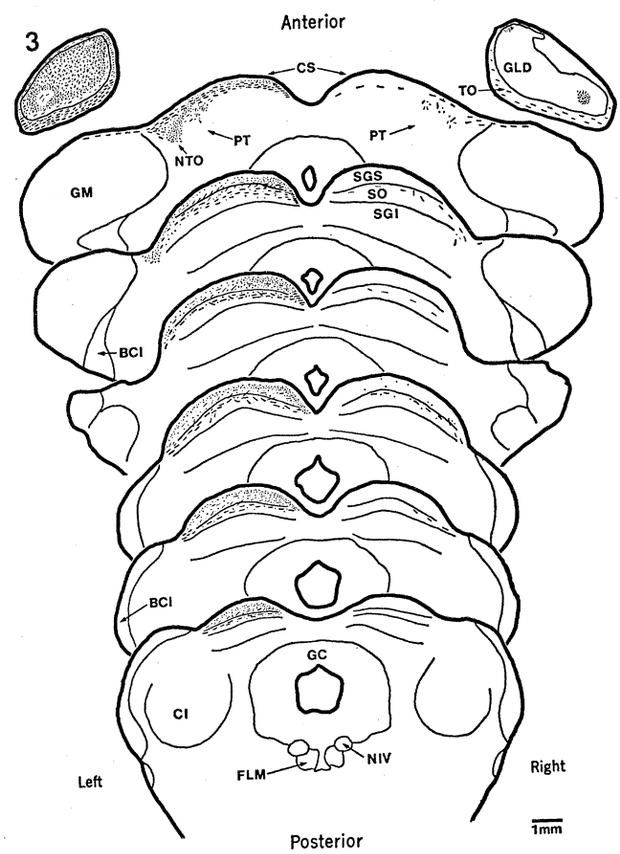




Fig. 2 (left). Drawings of degenerating retinal axons (dashed lines) and preterminals and terminals (dots) at various levels through the thalamus and pretectum of the Siamese cat. Left side of figure is contralateral to the enucleation. *BCI*, brachium inferior colliculus; *GC*, central gray; *GLD*, dorsal lateral geniculate; *GM*, medial geniculate; *GLV*, ventral lateral geniculate; *LP*, lateral posterior nucleus; *MD*, medial dorsal nucleus; *NIM*, medial interlaminar nucleus; *NIII*, oculomotor nucleus; *NR*, red nucleus; *NTO*, nucleus of optic tract; *PC*, posterior commissure; *PED*, cerebral peduncle; *PT*, pretectum; *PUL*, pulvinar; *TO*, optic tract. Fig. 3 (right). Drawings to show degenerating retinal axons (dashed lines) and preterminals and terminals (dots) at various levels through the posterior pretectum and superior colliculus. Left side of the figure is contralateral to the enucleation. *CS*, superior colliculus; *CI*, inferior colliculus; *FLM*, medial longitudinal fasciculus; *NIV*, trochlear nucleus; *SGS*, superficial gray layer; *SGI*, intermediate gray layer; *SO*, optic layer. Other abbreviations as in Fig. 2.

squint is also suggested by the differences between the dorsal lateral geniculate neurons, this abnormality should an ordinary cat in which squint has been induced artificially after birth. In the latter case, there is no disorganization of the laminae in the lateral geniculate (*16*).

Although the anomaly in the retinogeniculate pathway is especially prominent, in part because it involves a marked rearrangement of lateral geniculate neurons, this abnormality should not diminish the fact that the projection of the retina to the pretectum and superior colliculus is almost entirely crossed. Thus, any single factor responsible for the neuroanatomical defect cannot be specific to the formation of retinogeniculate connections.

We wish to emphasize that all of the major retinal pathways in the Siamese cat are abnormal (*17*). As a result, this animal must possess but a limited ability to process spatially correlated binocular information, with a consequent loss of stereoscopic depth perception. Any residual ability for stereoscopic depth perception must depend almost solely on the remaining ipsilateral input to the lateral geniculate nucleus, for the ipsilateral projections to the pretectum and superior colliculus are meager or absent. Thus, the limited ipsilateral retinogeniculate projection would appear to be the most significant factor in providing binocular information for the control of symmetrical eye movements (*18*).

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## Interocular Apparent Movement in Depth: A Motion Preference Effect

Abstract. *A new phenomenon is reported in which alternate stimulation of either nasal or temporal hemiretinas produces, respectively, apparent oscillation in depth either behind or ahead of the frontal plane. This control over the perceived movement is dependent on the proper positioning of stimuli presented interocularly and in horizontal arrangements.*

Apparent or stroboscopic movement is perceived when two separate visual stimuli are presented successively. This report describes a new apparent movement phenomenon which occurs when stimuli eliciting apparent movement in depth are presented interocularly. When the two triangles of Fig. 1A are alternately presented, the observer generally perceives a single triangle moving to and fro in depth about a vertical axis (*1*). The situation is ambiguous, since the vertex of the triangle, which appears to swing through an arc of about 180°, may oscillate either ahead of or behind the frontal plane. However, an experiment revealed that the type of movement perceived may be brought under control when the triangles are presented interocularly (each eye is stimulated by only one of the two triangles).

Two arrangements for presenting stimuli interocularly are illustrated in Fig. 1B. When the right and left figures are combined stereoscopically, the vertical fixation lines fuse and a triangle is perceived on each side. Although the visual fields for the upper and lower arrangements appear the same, the upper arrangement gives rise to stimulation of the two nasal hemiretinas and the lower arrangement gives rise to stimulation of the two temporal hemiretinas. In the experiment, 55 undergraduates individually viewed two stimulus cards in a Brewster stereoscope. The two cards each contained a nasal and temporal arrangement, but differed with respect to the position on the card (upper or lower) of each arrangement. The figures were white, 1.27-cm equilateral triangles on a black background. The right and left figures were each illuminated from behind by a separate neon bulb. Each bulb was illuminated for 500 msec; the interval between presentations was ap-

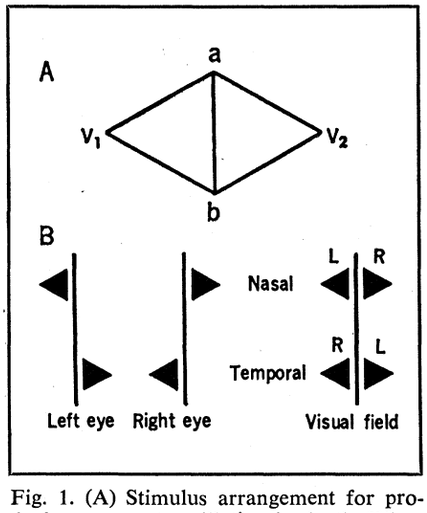


Fig. 1. (A) Stimulus arrangement for producing apparent oscillation in depth. When triangles $abV_1$ and $abV_2$ are alternately presented, the vertex of a single triangle oscillates between $V_1$ and $V_2$ about axis $ab$. (B) Arrangements for producing stimulation of nasal and temporal hemiretinas. Fixation is on the vertical line between the L (left-eye) and R (right-eye) triangles.