EVOKED POTENTIAL ESTIMATES OF VISUAL ACUITY OF SIAMESE CATS

A Thesis

Presented to

the Faculty of the Department of Physiological Optics University of Houston

> In Partial Fulfillment of the Requirement for the Degree Master of Science

> > By: Roger Lynn Boltz August, 1977

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ABSTRACT

It is known that the Siamese cat has a neurological anomaly of its visual system which results in temporal retinal fibers crossing at the optic chiasm instead of remaining ipsilateral as they do in normal cats. This results in a disruption of the normal retinotopic projection to both the lateral geniculate nucleus and the cortex. At the cortex, Siamese cats show a significant lack of binocularity compared to normal cats. Because of these abnormalities, the visual function of the Siamese cat may be different from normal cats. Electrophysiological methods were used in this study to obtain estimates of visual acuity and contrast sensitivity for the Siamese cat. Using established evoked potential techniques, it was determined that Siamese cats have lowered acuity and contrast sensitivity functions compared to normal cats.

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CHAPTER I

INTRODUCTION

It is generally known that Siamese cats are often cross-eyed. Hyde (1962), in a study of this condition suggested that this recessive characteristic may be associated with innervational abnormalities.

Guillery (1969) confirmed this abnormality by showing that layer Al of the lateral geniculate body, which contains fibers from the retina of the ipsilateral eye in the normal cat, has an abnormal representation of fibers from the retina of the contralateral eye in addition to fibers from the ipsilateral eye. This results in an abnormally large contralateral eye representation and a small ipsilateral eye representation at the level of the lateral geniculate nucleus. He suggested that this may have resulted from an abnormal crossing of some fibers from the temporal retina of the contralateral eye.

The lateral geniculate body of the normal can be divided into three layers as shown in Figure 1. Studies (Hayhow, 1958; Bishop, Kozak, Levick, and Vakkur, 1962; Stone and Hansen, 1966) have shown that layer A, the most dorsal layer, receives nasal retinal fibers from the contralateral eye. Layer A1 receives temporal retinal fibers from the ipsilateral eye. Layer B is thought to contain fibers from the nasal retina of the contralateral eye. It should be noted that Guillery (1970) has reclassified the area ventral to layer A1 as layers C, C1, and C2. Layer C receives contralateral fibers while layer C1 receives ipsilateral fibers. Layer C2 is thought to contain fibers passing through to other lamina.

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Schematic of lateral geniculate body of the normal cat as seen in frontal section.



In addition to this laminar arrangement, it has been found that adjacent areas in layers A and AI have their receptive fields in approximately the same visual field location (Bishop, Kozak, Levick and Vakkur, 1962). That is, there are columns which run down and backwards through layers A and A1, in which the cells have receptive fields in the same place in the visual field.

Hubel and Wiesel (1971) studied the projections of the Siamese cat using electrophysiological methods. They found that the abnormal segments of layer A1 contained cells with projections from the temporal retina of the contralateral eye.

Guillery and Kaas (1971) made a more detailed investigation of the retinogeniculate projections of Siamese cats. They found that the retinal projections to layer A were the same as in normal cats. In layer A1, however, they found areas of aberrant input from the contralateral eye as shown schematically in Figure 2. The most lateral segment of layer A1 contains normal projections from the ipsilateral eye. More medial to this is a large area of abnormal representation from the contralateral eye, while more medial still, is again, a small normal representation from the ipsilateral eye.

Electrophysiological data from Guillery and Kaas (1971) show the retinotopic organization of the Siamese cat. Their findings may be represented in a schematic drawing (Figure 3). Moving laterally in layer A of the normal cat's lateral geniculate body means that the receptive field position in the contralateral visual field, also moves laterally. This is also true for layer A of the Siamese cat. Movement laterally in layer A1 of the normal cat's LGN means that the receptive field position in the contralateral visual

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Schematic of lateral geniculate body of the Siamese cat as seen in frontal section.



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Schematic representation of retinogeniculate projections in normal and Siamese cats. The symbols \bigcirc and \bigtriangleup represent the eye supplying input to each LGN segment. Clear areas \square represent normal input. Striped areas \blacksquare represent abnormal input. (After Guillery and Casagrande, 1975a).



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field also moves laterally. In Siamese cats, lateral movement through the normal segments of layer A1 represents normal lateral movement of receptive field positions in the contralateral visual field. However, in the abnormal segment of layer A1 of the Siamese cat, indicated by the diagonal lines in Figure 3, lateral movement in the LGN means lateral movement of receptive fields in the ipsilateral visual hemifield.

The receptive fields of cells within the abnormal segments of layer A1 lie in a 20° wide vertical strip of the ipsilateral visual hemifield. The medial edge of this strip is close to the vertical meridian.

The projection to the visual cortex of the abnormal segments has been the subject of several studies. Creel (1971) demonstrated a weak evoked potential when the ipsilateral eye of Siamese cats was stimulated, suggesting a decrease in cortical input from the ipsilateral eye, and a strong evoked potential when the contralateral eye was stimulated. In contrast, normal cats showed strong evoked potentials with either contralateral or ipsilateral stimulation.

Hubel and Wiesel (1971) recorded from cortical units in the Siamese cat. Of the 303 cells recorded, only 14 were driven from the ipsilateral eye. Additionally, no binocularly driven cells were found, with the exception of 4 cells from a kitten which had had binocular lid sutures since birth.

Hubel and Wiesel also found that in Siamese cats, the ipsilateral visual field out to approximately 20[°] was represented at the visual cortex. In normal cats, only the contralateral visual field is represented at cortex.

Thus it would seem that the aberrant temporal retinal fibers from the contralateral eye are projected to the cortex, giving an additional 20⁰ of visual field representation. This may be schematically represented by

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Figure 4. In addition, the amount of cortical input from the ipsilateral eye is considerably reduced, as shown by the small numbers of cells which can be driven by that eye.

Kaas and Guillery (1973) have also recorded from cortical units in Siamese cats. They also found that there was greatly reduced input from the ipsilateral eye. However, contrary to the findings of Hubel and Wiesel (1971), they found very little representation of the ipsilateral visual field at the cortex. It would appear that the abnormal input from the contralateral eye is largely suppressed rather than represented as Hubel and Wiesel found. The pattern of cortical representation found by Kaas and Guillery is shown in Figure 5.

Thus, there appear to be two types of cortical abnormality associated with Siamese cats. One, the "Boston" pattern, Figure 4, of Hubel and Wiesel shows a representation of the abnormal input. The other "Midwestern" pattern, Figure 5, of Kaas and Guillery shows a suppression of the abnormal input.

These two patterns may be related to the degree of strabismus. Cool and Crawford (1972) found that strabismic Siamese cats showed ipsilateral visual field representation at the cortex while orthophoric Siamese cats showed very little ipsilateral visual field representation at the cortex. Additionally, the less the strabismus, the less the ipsilateral visual field representation that was found. All penetrations were made near the 17/18 border.

Their results indicate that strabismic Siamese cats show "Boston" type patterns and orthophoric Siamese cats show "Midwestern" type patterns. The cats in Hubel and Wiesel's study were esotropic and those of Kaas and Guillery's study were orthophoric.

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Schematic representation of projections to the visual cortex of normal and Siamese cats (Hubel and Wiesel, 1971). Note the additional representation of the ipsilateral visual field seen in the Siamese cat's visual cortex. Symbols \bigcirc and \triangle denote eye supplying input. Striped areas, $\boxed{22}$, indicate abnormal input. Clear areas, \square , denote normal input. (After Guillery, 1974).



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Schematic representation of projections to the visual cortex of normal and Siamese cats (Kaas and Guillery, 1973). Note the lack of additional input of the ipsilateral visual field in this Siamese cat's visual cortex as compared to that in Figure 4. The difference between this Siamese cat's cortex and the normal cat's cortex is the lack of input from the ipsilateral eye. Symbols, \bigcirc and \triangle denote the eye supplying input. Striped areas, \square , indicate abnormal input. Clear areas, \square , denote normal input. (After Guillery, 1974).



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Very recently, Shatz (1977) has studied "Boston" and "Midwestern" Siamese cats. She found that the medial normal segment of layer A1 of the lateral geniculate body of "Boston" Siamese cats was small compared to "Midwestern" Siamese cats. This correlated with the cortical findings previously described. However, Shatz was not able to find a clear relationship between the strabismus of these cats and the organization of the lateral geniculate body.

The visual system anomaly associated with Siamese cats has been suggested to be associated with albinism (Creel, 1971). This seems very likely since other albino animals, such as rats, mice, guinea pigs, rabbits, ferrets, minks, tigers, and humans, have shown similar neurological abnormalities (Lund, 1965; Guillery, Sitthi-Amorn, and Eighmy, 1971; Westenburg and Giolli, 1973; Guillery, 1972; Giolli and Creel, 1973; Sanderson, 1972; Guillery, 1971; Sanderson, Guillery, and Shackelford, 1974; Guillery and Kaas, 1973; Guillery, Kaas, and Whitkop, 1975).

It becomes of interest to discover how these neurological abnormalities affect the visual functions of Siamese cats. Studies have been made dealing with this question.

Elekessy, Campion, and Henry (1973) studied the visual fields of Siamese cats with behavioral techniques. Studying four orthophoric and two esotropic cats, they found nasal visual field losses for all cats. The Siamese cats were unable to see in areas of the nasal field $(15^{\circ}-30^{\circ})$ where normal cats were able to see.

These authors interpreted this field loss to be caused by suppression of input. It is the type of field loss that would be expected on the basis of electrophysiological investigations.

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Another visual function which may be tested is resolution, i.e., acuity and contrast sensitivity. These functions may be tested both by behavioral and electrophysiological methods.

Campbell and Maffei (1970) opened the area of contrast sensitivity measurements to electrophysiology. They showed that the psychophysical contrast threshold of sine wave gratings in humans could be predicted from evoked potential measurements. For each of several different spatial frequencies, they found a linear relation between the amplitude of the evoked potential and the log of the contrast. By extrapolating to zero measured evoked potential amplitude the regression line between log contrast and evoked potential amplitude, they could predict the psychophysical thresholds for man.

Berkley and Watkins (1971) used a similar technique to obtain an estimate of the acuity function of the normal cat. Using alternating square wave gratings of fixed contrast (0.62-0.82) as stimuli, they recorded evoked potentials. By measuring the amplitude of the evoked potentials to gratings of different spatial frequencies, a linear relationship was found between the amplitude of the evoked potential and the logarithm of the spatial frequency. Extrapolating the amplitude of the measured evoked potential to zero amplitude, they estimated the acuity of the cat to be between 5.0 and 5.9 cycles/degree.

Later, in another study (Berkley and Watkins, 1973), they estimated the acuity of the cat to be 3.9 cycles/degree for sine wave gratings with a contrast of 0.50. They attributed this lower value to lower contrast and mean luminance levels.

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Campbell, Maffei and Piccolino (1973), using evoked potentials, determined the contrast sensitivity curve of the cat. They used as a stimulus, sinewave gratings which alternated back and forth by one-half cycle at a frequency of 8 Hz. They found a linear relationship between the amplitude of the evoked potential and logarithm of the contrast for each spatial frequency used. Extrapolating the evoked potential amplitude to zero, they obtained a contrast threshold for each spatial frequency used. From these threshold values they obtained a contrast sensitivity curve.

The results of Campbell, et al. (1973) may be seen in Figure 6. They found that the peak contrast sensitivity of the cat was lower in spatial frequency than man's by about a factor of ten. Below 0.5 cycles/degree, the cat's contrast sensitivity is higher than man's. Above this spatial frequency it is lower.

Blake, Cool, and Crawford (1974) were able to determine the visual resolution of the cat using behavioral techniques. Using conditioned suppression techniques, they determined the visual resolution of the cat to be 6 cycles/ degree for sinusoidal gratings with a contrast of 0.75. This value agrees quite well with the results of Berkley and Watkins (1971, 1973).

Muir and Mitchell (1973), also using behavioral techniques, obtained estimates of resolution for cats of about 3 cycles/degree for square wave gratings.

Blake, Cool and Crawford (1974) and Bisti and Maffei (1974) have obtained behavioral measurements of contrast sensitivity for the cat. Their results are quite close to those Campbell, <u>et</u> al. (1973) obtained electrophysiologically. There are, however, some differences between the results

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Contrast sensitivity of the normal cat, three animals shown by the filled symbols. The open circles represent human psychophysical data. The thick line is the optical transfer function of the cat. (From Campbell, et al., 1973).



of Blake, <u>et al.</u> (1974) and those of Campbell, <u>et al.</u> (1973). The Blake, <u>et al.</u> data shows a higher peak spatial frequency and faster decline of sensitivity in the higher spatial frequencies than does the Campbell, <u>et</u> al. data.

Studies of single ganglion, lateral geniculate, and cortical cells (Enroth-Cugell and Robson, 1966; Campbell, Cooper, and Enroth-Cugell, 1969; Maffei and Fiorentini, 1973) have shown no units which respond to gratings with spatial frequencies higher than 5 cycles/degree. This corresponds well to the acuity values found by both the evoked potential and behavioral methods.

Additionally, Wässle (1971), using the modulation transfer function of the cat's eye, calculated the minimum separable distance for two parallel slits to be resolved would be 4-5 minutes of arc. This value corresponds to spatial frequencies of 6-7.5 cycles/degree, a value only slightly higher than those obtained by the above studies.

Recent data, however, suggests that the acuity of the cat may be better than previously reported. Jacobson, Franklin, and McDonald (1976), using behavioral techniques, have found binocular grating acuity for square wave gratings to be 8-9 cycles/degree.

Other studies also support higher resolution limits for the cat (Ikeda and Wright, 1973; Enroth-Cugell and Robson, 1974; Robson, 1976; Steinberg, Reid, and Lacy, 1973).

The Siamese cat, because of its neurological abnormalities, may have different visual function than the normal cat. Packwood and Gordon (1975), however, found the behaviorally, both normal and Siamese cats had acuity

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of 6' of arc or about 5 cycles/degree. On the other hand, very recent data from Blake and Antoinetti (1976) shows that Siamese cats have lower contrast sensitivity than do normal cats (Figure 7). Using behavioral methods, they found the cutoff frequency to be about 1.8-2.3 cycles/degree. This is considerably lower than that found for the normal cat.

The purpose of the project was to determine, by electrophysiological methods, if the visual acuity of the Siamese cat was abnormal. Specifically, does the abnormal visual pathway cause the acuity of the Siamese cat to be any different than that of ordinary cats? The anomaly associated with the Siamese cat certainly limits the possibility of this type of cat having binocular vision. Does it also cause a reduction in visual acuity?

Contrast sensitivity of normal and Siamese cats. Open squares represent data from a normal cat. Filled triangles and circles represent data from two Siamese cats. (From Blake and Antionetti, 1976).

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CHAPTER II

METHODS

Three adult Siamese cats and three normal control cats were used as acute preparations. The Siamese cats were chosen by their typical fur color and blue irises. An estimate of the ocular alignment of each cat was made using the corneal reflex test while the cat looked at a distant object.

Each cat was weighed (weight range 1.5-2.5 Kg.) and anesthetized with sodium pentobarbitol (35 mg/kg) injected intraperitoneally. A subcutaneous injection of atropine (lcc) was also given to prevent fluid accumulation in the lungs. The cat's head was shaved and a midline incision was made at the top of the scalp. The skin and muscle was retracted to expose the skull. After localization of the approximate area of the posterior lateral gyrus by means of skull sutures, a hole was cut into the skull with a 1 cm trephine. The bone plug was removed, dura exposed and the hole was then lightly covered with bone wax. Two small holes were drilled onto the anterior skull over the frontal sinuses. A head holder was attached here with screws.

The animal was placed on a shielded table and was supported by the head holder. It was tracheotemized and artificially respirated with a mixture of 45% oxygen inspired air. Flaxedil (7 mg/Kg/hr) was given intravenously to prevent eye movements. The cat's EKG was monitored and its body temperature was maintained at 38.5° C using a thermistor controlled, D.C. powered heating pad.

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Local anesthesia of all wounds was maintained by injections of Xylocaine.

The cat's nictitating membranes were retracted with 10% phenylephrine hydrochloride. Refraction was performed by retinoscopy with trial lenses and the cat was then corrected with spherical power contact lenses for the viewing distance of 57 cm.

The bone wax covering the hole in the skull was removed and a piece of Gelfoam was placed on the dura. A gold cup electrode was then placed on the Gelfoam and the hole was sealed over with bone wax.

The electrode was attached to a differential pre-amplifier (PAR 113) referenced to ground. The amplified signals were then fed to a Nicolet signal averaging computer, displayed on an oscilloscope, and printed by an X-Y plotter.

The area centralis of the cat was identified ophthalmoscopically according to the methods of Vakkur, Bishop, and Kozak (1963) and projected by a projection ophthalmoscopic technique (Fernald and Chase, 1971) onto a tangent screen 57 cm. away.

The eye ipsilateral to the electrode was occluded and an oscilloscope (P4 phosphor, Tektronex) was placed at the projected area centralis, 57 cm. away from the cat. The oscilloscope screen was masked down to 13° horizontally and 5° vertically.

A sinusoidally modulated vertical grating was produced on the oscilloscope screen in the usual manner using two function generators (Campbell and Green, 1965). The contrast of the grating was controlled by varying the amplitude of the Z-axis modulation signal.

The grating was caused to shift back and forth by one-half cycle at a rate of 3 Hz by alternating between a sine and inverted sine wave

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grating. This was accomplished by having a function generator inputting into a Schmitt trigger which caused the shift between a sine and inverted sine wave. This shift also served as the trigger for the signal averager.

An alternation rate of 3 Hz was chosen empirically as the rate which gave the largest and most consistent evoked potentials.

The mean luminance and contrast levels were measured by a Pritchard photometer.

Each cat was shown gratings starting with low spatial frequencies and high contrasts. The spatial frequencies were then increased for a given contrast level.

In the experiments with the Siamese cats, several different contrast levels were used. In addition, several control records were taken with both the normal and Siamese cats by obtaining evoked potentials to a stimulus screen with no grating.

The evoked potential from the differential pre-amplifier (band pass 0.3-30 Hz) was then filtered by a notch filter which as set to pass a 6 Hz signal. This frequency signal was chosen because it was twice the frequency of alternation of the stimulus (3 Hz) used in these experiments. Previous studies (Berkley and Watkins, 1971, 1973; Campbell, Maffei, and Piccolino, 1973) have also filtered the evoked potential to obtain a frequency twice the alternation rate of the stimulus. This signal was then fed into the signal averager where 512 averages were obtained for each evoked potential. The length of time for each sample record of the average was 400 msec.

This procedure gave an evoked potential which resembled a sine wave and was thus easy to measure. The amplitude of the evoked potential was

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measured from peak to trough. Figure 8 shows a typical evoked potential and the measuring points.

At the end of each recording session, each Siamese cat was sacrificed by injecting it intravenously with sodium pentobarbitol and perfusing it with 10% formalin. The brains of these cats were then removed and 50 μ m frozen sections were cut in the frontal plane. The sections were stained with cresyl violet and examined for the presence of the geniculate anomaly known to be present in Siamese cats (Guillery, 1969).

Typical evoked potential record. Peak to trough measurements were made as shown on the waveform.



CHAPTER III

RESULTS

Figure 9 shows the calibration of contrast for different potentiometer settings. The potentiometer controlled the contrast of the grating by varying the amplitude of the Z-axis modulation signal. Contrast was defined as $\frac{L_{max} - L_{min}}{L_{max} + L_{min}}$, where L_{max} and L_{min} are the maximum and minimum

luminance values, respectively, of the screen. The luminance values were measured in candelas/m² by a Pritchard photometer using a 2' diameter spot. Each data point in Figure 9 is the average of contrast levels calculated for four spatial frequencies: 0.125, 0.25, 0.50, and 1.0 cycles/degree. Standard deviations are shown as bars.

Each measurement was made of a square wave grating due to the fact that the smallest measuring diameter of the photometer was 2' of arc. Measuring a sine wave grating with this size measuring spot would have resulted in a calculated contrast level which would have been lower than the actual contrast, because the measurement would not have been of the high and low luminance points, but an average over an area in which the luminance was constantly changing.

As can be seen from Figure 9, there was a good linear relation between the potentiometer setting and the calculated contrast.

In order to verify that the contrast obtained for the square wave grating was the same as that obtained for the sine wave grating, the voltage

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Contrast $\left(\frac{L_{max} - L_{min}}{L_{max} + L_{min}}\right)$ of the grating as a function of the

potentiometer setting.

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POTENTIOMETER SETTING

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modulation (peak to trough) of the input to the Z-axis of the display oscilloscope was measured. The results are seen in Table 1. As can be seen here, the voltage modulation was slightly higher at high contrast levels, for the square wave gratings than for the sine wave gratings. However, this difference was only about 0.2 volts and would result in a contrast difference of approximately 0.02. The difference was less at lower contrast levels.

Mean luminance levels for different contrast values were measured with the Pritchard photometer using a 1° measuring area for spatial frequencies of 1 cycle/degree and above. Mean luminance values for spatial frequencies of 0.125-0.50 were calculated by averaging the light bar and dark bar luminance measurements used to calculate contrast.

The mean luminance values for different contrast levels is shown in Figure 10. Each mean luminance level is the average of all spatial frequencies measured and standard deviation bars are shown. The overall average mean luminance level was 13.64 cd/m².

As can be seen from Figure 10, the mean luminance does not change significantly from one contrast level to another. However, there is some change in mean luminance level between spatial frequencies as evidenced by the standard deviations. Most of this variation comes from the spatial frequencies, 0.12-0.50 cycles/degree. As can be seen in Table 2, these luminance levels are lower than those for spatial frequencies above 0.50 cycles/ degree. This difference is probably due to a difference in measuring techniques for the spatial frequencies of 0.12-0.50 cycles/degree.

However, most importantly, the mean luminance of the screen did not change as the grating shifted between a sine and inverted sine wave.

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TABLE 1

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Contrast of sine wave and square wave gratings for different potentiometer settings at various spatial frequencies. Contrast was determined by measuring the peak to trough voltage difference of the input to the Z-axis of the display oscilloscope.

TABLE 1

Potentiometer	0.12	c/deg	0.25	c/deg	0.50	c/deg	1.0 0	c/deg
Setting	sine	square	sine	square	sine	square	sine	square
	wave	wave	wave	wave	wave	wave	wave	wave
1000	4.6	4.8	4.6	4.8	4.6	4.7	4.6	4.8
900	4.0	4.2	4.0	4.1	4.0	4.1	4.1	4.1
800	3.4	3.6	3.4	3.6	3.4	3.6	3.5	3.5
700	3.0	3.0	3.0	3.0	2.9	3.0	3.0	3.1
600	2.5	2.6	2.5	2.6	2.5	2.6	2.5	2.6
500	2.1	2.2	2.2	2.2	2.1	2.2	2.1	2.2
400	1.7	1.7	1.7	1.7	1.7	1.7	1.7	1.8
300	1.3	1.3	1.3	1.3	1.3	1.3	1.3	1.3
200	0.9	0.9	0.9	0.9	0.9	0.9	0.8	0.9
100	0.4	0.5	0.4	0.5	0.4	0.5	0.4	0.5
50	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2
0	0	0	0	0	0	0	0	0

Potentiometer Setting	2.0 sine wave	c/deg square wave	3.0 c/deg sine wave	4.0 c/deg sine wave	5.0 c/deg sine wave	6.0 c/deg sine wave	8.0 c/deg sine wave
1000	4.5	4.7	4.5	4.5	4.5	4.4	4.4
900	3.9	4.0	3.9	3.9	3.9	3.8	3.8
800	3.2	3.5	3.3	3.4	3.3	3.3	3.3
700	2.9	3.0	2.9	2.9	2.8	2.8	2.8
600	2.4	2.6	2.4	2.4	2.4	2.4	2.4
500	2.1	2.1	2.0	2.0	2.0	2.0	2.0
400	1.7	1.7	1.7	1.6	1.6	1.6	1.7
300	1.2	1.3	1.3	1.3	1.2	1.2	1.2
200	0.8	0.9	0.8	0.8	0.8	0.8	0.8
100	0.4	0.5	0.4	0.4	0.4	0.4	0.4
50	0.2	0.2	0.2	0.2	0.2	0.2	0.2
0	0	0	0	0	0	0	0

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Mean luminance of the oscilloscope as a function of the contrast of the grating. Standard deviation bars are shown. MEAN LUMINANCE (cd / m²)



TABLE 2

Mean luminance levels of oscilloscope for different spatial frequencies at different contrast levels (as indicated by potentiometer dial settings). All measurements are in candelas/m² and are taken with a 1° diameter measuring spot.

TABLE 2

Potentiometer Setting	0.12 c/deg	0.25 c/deg	0.50 c/deg	1.0 c/deg
1000	12.08	11.44	12.60	13.72
900	12.13	11.47	12.76	13.74
800	11.94	11.15	12.38	13.75
700	11.66	10.94	12.28	13.75
600	11.46	10.82	12.20	13.86
500	11.32	10.70	12.06	13.94
400	11.22	10.68	11.98	14.04
300	11.18	10.68	12.00	14.14
200	11.22	10.70	12.07	14.27
100	11.30	10.80	12.20	14.47
50	11.39	10.84	12.21	14.55
0	11.45	10.90	12.32	14.67

Potentiometer Setting	2 c/deg	3 c/deg	4 c/deg	5 c/deg	6 c/deg	8 c/deg
-	-	U	Ŭ	. 0	. 0	
1000	14.37	14.72	14.95	15.29	15.15	15.18
900	14.27	14.59	14.85	15.16	15.01	15.03
800	14.16	14.45	14.69	14.97	14.80	14.83
700	14.06	14.33	14.55	14.81	14.64	14.66
600	14.02	14.26	14.47	14.71	14.52	14.56
500	14.02	14.22	14.42	14.65	14.45	14.48
400	14.06	14.22	14.41	14.64	14.44	14.44
300	14.12	14.27	14.45	14.66	14.46	14.45
200	14.23	14.36	14.53	14.75	14.53	14.64
100	14.39	14.52	14.68	14.89	14.67	14.80
50	14.49	14.62	14.77	14.97	14.76	14.92
0	14.61	14.93	14.89	15.09	14.79	15.05

Potentiometer Setting	Average <u>+</u> S.D.
1000	13.95 + 1.42
900	13.90 + 1.33
800	13.71 + 1.38
700	13.57 + 1.41
600	13.49 + 1.44
<i>5</i> 00	13.43 + 1.48
400	13.41 + 1.50
300	13.44 + 1.53
200	13.53 + 1.56
100	13.67 + 1.59
50	13.75 + 1.61
0	13.87 ± 1.64

The acuity function of three normal control cats is shown in Figures 11-13. These acuity functions were derived after the methods of Berkley and Watkins (1971, 1973). Each evoked potential amplitude, measured peak to trough, was measured in arbitrary units. For the contrast of 0.72, each amplitude was then scaled relative to the largest amplitude, 1.0. This relative value was then plotted as a function of its spatial frequency. The curves were fit by linear regression for spatial frequencies of 0.25 cycles/degree and higher. Spatial frequencies lower than 0.25 cycles/degree were fit by eye.

As can be seen from Figures 11-13, each graph shows a maximum at 0.125 cycles/degree. From this value, the graph slopes in a relatively linear fashion toward zero relative evoked potential amplitude.

By extrapolating the regression line to zero evoked potential amplitude, an estimate of acuity was obtained. This was found by taking the spatial frequency at which the graph reached the zero relative evoked potential amplitude.

The estimated acuity was 9.0 cycles/degree for cat N-2, 1.4 cycles/ degree for cat N-3, and 2.9 cycles/degree for cat N-4.

These values, exept for cat N-3, are within the range obtained by Berkley and Watkins (1973). Interestingly, cat N-3 was the only hyperopic cat (+2.50) of the six cats tested. Possibly this cat had amblyopia associated with the hyperopia, as is often seen in humans. It is also possible that the refraction of this cat was in error.

The acuity functions of three Siamese cats are shown in Figures 14-16. Acuity estimates were derived as above. Confirmation of these cats

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Relative evoked potential amplitude as a function of spatial frequency of the grating. The grating contrast was 0.72. Solid line is linear regression line. Interrupted line is a fit by eye. See text for further details.



SPATIAL FREQUENCY (cycles/deg.)

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Relative evoked potential amplitude as a function of spatial frequency of the grating. The grating contrast was 0.72. Solid line is linear regression line. Interrupted line is a fit by eye. See text for further details.



SPATIAL FREQUENCY (cycles/deg.)

-44-

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Relative evoked potential amplitude as a function of spatial frequency of the grating. The grating contrast was 0.72. Solid line is linear regression line. Interrupted line is a fit by eye. See text for further details.



SPATIAL FREQUENCY (cycles/deg.)

Relative evoked potential amplitude as a function of spatial frequency of the grating. The contrast of the grating was 0.72. Solid line is a linear regression fit of data. See text for further details.



SPATIAL FREQUENCY (cycles/deg.)

Relative evoked potential amplitude as a function of spatial frequency of the grating. The grating contrast was 0.72. Solid line is linear regression line. Interrupted line is a fit by eye. See text for further details.



SPATIAL FREQUENCY (cycles/deg.)

Relative evoked potential amplitude as a function of spatial frequency of the grating. The grating contrast was 0.72. Solid line is linear regression line. Interrupted line is a fit by eye. See text for further details.



SPATIAL FREQUENCY (cycles/deg.)

being Siamese was made by histological verification of the geniculate anomaly for cats S-1 and S-3. Unfortunately, the tissue from cat S-2 was not suitable for sectioning. The data for cat S-1 was fit by linear regression line for spatial frequencies of 0.125 and higher because of the small number of data points. The acuity was 2.0 cycles/degree for cat S-1, 0.8 cycles/degree for cat S-2, and 3.9 cycles/degree for cat S-3. All of these values are lower than those for the normal cats, with the exception of cat N-3 and cat S-3.

The spatial frequency associated with the maximum relative evoked potential amplitude is more variable for the Siamese cats than for the normal cats. Cat S-1 shows no low frequency roll-off as do all the other cats, probably because this cat was not tested below 0.125 cycles/degree, the peak sensitivity for most of the cats tested here. Cat S-2 shows a broad peak around 0.25 cycles/degree, although it could lie between 0.125 and 0.25 cycles/degree. Cat S-3 shows a peak at 0.125 as do all the normal cats.

The correlation coefficient for each of the regression line in Figures 11-16 was -0.93 or better. This indicates a good linear relation between relative evoked potential amplitude and spatial frequency.

As can be seen, the acuity estimate derived this way shows the Siamese cats to have lower acuity than the normal controls, with the exception of cat N-3, whose low acuity was discussed earlier, and cat S-3 which showed a high acuity function. The acuity of cat S-3 estimated from Figure 16 places it in the range of normal cats. This high value of acuity will be discussed later.

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An attempt was made to obtain contrast sensitivity functions for the Siamese cats using the methods of Campbell, Maffei, and Piccolino (1973).

To do this, evoked potential amplitude, in arbitrary units, was plotted versus contrast on a log scale. This was done for each spatial frequency and is shown in Figures 17-19. The data were fit by linear regression techniques and these lines were extrapolated to zero evoked potential amplitude. The contrast value corresponding to zero evoked potential amplitude was taken as the threshold value.

These contrast threshold values were then plotted in Figure 20 as contrast sensitivity (1/threshold contrast) versus spatial frequency. The data for all three Siamese cats is shown in Figure 20. A curve is fitted through the data by eye. Although there is much variability in the data, there is a clear decrease in contrast sensitivity with increasing spatial frequency. It is estimated from this graph, that the high frequency cutoff would be slightly less than 2 cycles/degree.

Relative evoked potential amplitude as a function of contrast of the grating for several spatial frequencies. Linear regression curves are drawn for each spatial frequency. The cut-off point, contrast level where relative evoked potential amplitude fell to zero, was calculated from the equation for each line. The correlation coefficient for each spatial frequency is 0.99 for 0.125 c/deg., 0.94 for 0.25 c/deg. and 0.69 for 0.50 c/deg.



Relative evoked potential amplitude as a function of contrast of the grating for several spatial frequencies. Linear regression curves are drawn for each spatial frequency. The cut-off point, contrast level where relative evoked potential amplitude fell to zero, was calculated from the equation for each line. The correlation coefficient for each spatial frequency is 0.88 for 0.09 c/deg., 0.91 for 0.125 c/deg., 0.82 for 0.25 c/deg., and 0.90 for 0.365 c/deg.





Relative evoked potential amplitude as a function of contrast of the grating for several spatial frequencies. Linear regression curves are drawn for each spatial frequency. The cut-off point, contrast level where relative evoked potential amplitude fell to zero, was calculated from the equation for each line. The correlation coefficient for each spatial frequency is 0.82 for 0.09 c/deg., 0.95 for 0.125 c/deg., 0.95 for 0.25 c/deg., 0.83 for 0.365 c/deg., 0.71 for 0.50 c/deg., and 0.80 for 0.75 c/deg.



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Contrast sensitivity data for the three Siamese cats. Each data point was determined from Figures 17-19 as described in the text. The curve was fitted by eye. The symbols are X - cat S-1, O - cat S-2, and □ - cat S-3.



CHAPTER IV

DISCUSSION

As can be seen from the data, the acuity functions of the Siamese cats were, in most cases, lower than those of the normal control animals. One control animal, N-3, however, showed poor acuity compared to the others and compared to the values published in the literature.

As was mentioned previously, this cat was the only cat which showed hyperopic (+2.50 D.S.) ammetropia. Two possible explanations of the acuity of this cat can be based on this refractive error. First, the cat may have suffered from anisometropic amblyopia. This well known form of amblyopia is due to unequal refractive error in the two eyes (von Noorden, 1967). The refractive status of the non-stimulated eye in this experiment was not measured by retinoscopy, so there is no way of testing this hypothesis.

It may also have been possible that the hyperopia, even if present bilaterally, could have resulted in a blurred retinal image if it were greater than the cat's accommodative ability. Several attempts at estimating the cat's amplitude of accommodation have been made (Morgan, Mohney, and Olmsted, 1943; Vakkur, Bishop, and Kozak, 1963; and Hughes, 1972). All but the estimates of Morgan, <u>et al</u>. (1943) place the amplitude of accommodation at 4-5 D or less. If this is the case, cat N-3 would have had to use at least one-half its accommodation to focus on objects at infinity. Objects closer than about 40 centimeters would be blurred for the cat. This might result in a deprivation type of amblyopia.

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A second possible explanation of this cat's poor acuity estimates is that the retinoscopic refraction was in error. Although this author has had a great deal of experience performing retinoscopy on humans, cats are more difficult to test. If the refractive correction used in this experiment was in error, the acuity estimates would most certainly have been too low (Campbell and Green, 1965).

A third possible reason for the low acuity estimate of this cat is that the measurements were in error. This seems unlikely since the same techniques were used for all cats, and only this cat of the normals showed acuity outside the ranges previously published.

Of course, the possibility remains that the acuity of this cat was low for some other, as yet unknown reason.

The acuity estimate for cat S-3 as determined from Figure 16, is higher than any of the estimates for the other Siamese cats. In fact, the value of 3.9 cycles/degree obtained from Figure 16 is within the range for normal cats.

The data are well fit by the curve in Figure 16. It appears however, that if data from 0.125 cycles/degree and higher were used to obtain the regression line, the cut-off frequency of this cat might be lower. This was done and the results are shown in Figure 21. The estimated acuity from this graph is 3.2 cycles/degree, considerably lower than the acuity estimated from Figure 16. The fact that the fit of the regression line was good (the correlation coefficient was -0.99) shows that this manipulation was justified.

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Replot of the data for cat S-3 for spatial frequencies of 0.125 c/deg. and higher. A linear regression line is drawn through the data. The purpose of this replot is discussed in the text.



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SPATIAL FREQUENCY (cycles/deg.)
The spatial frequency of 0.25 cycles/degree was chosen as the lowest spatial frequency represented in Figures 11, 12, 13, 15 and 16 only because the data appeared linear for this and higher spatial frequencies. The lowest spatial frequency could have been 0.125 cycles/degree without going beyond the apparently linear range, except for cat S-2 which showed a peak around 0.25 cycles/degree and cat N-4 which began to show a slight change in slope below 0.25 cycles/degree. Had the regression lines been drawn through the entire apparently linear range for each cat, only the cut-off frequencies for cats N-3 and S-3 would have been changed substantially. Cat S-3 showed a decrease in cut-off frequency, from 3.9 cycles/degree to 3.2 cycles/degree.

It thus appears that the best acuity estimate should be made by including the data from the entire apparently linear range. This was not done initially, however, to avoid the subjective evaluation of the linear range.

The data on contrast sensitivity of the Siamese cat obtained by this study conforms generally to that of Blake and Antoinetti (1976). The values of sensitivity found here are generally lower than their published values. However, they were working at a mean luminance of 60 cd/m^2 , while this study was done with a mean luminance of 14 cd/m^2 . This may be responsible for some of the difference since it is known that lowering the mean luminance of the grating lowers the contrast sensitivity of the subject (Patel, 1966). The high frequency cut-off of the combined data shown in Figure 20 does however, approach the high frequency cut-off of Blake and Antoinetti (1976). The data from the present study, however, is over such a small range of spatial frequencies that it is not realistic to make firm statements about it. The most positive statement that can be made is that the data from the two studies seem compatible.

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The present study shows that Siamese cats do have poorer visual resolution than do ordinary cats. The etiology of the poor acuity of the Siamese cat is unknown at this time. Blake and Antoinetti (1976) postulated that there may be more Y-cells (transient units) misdirected at the chiasm than X-cells (sustained units). Since sustained cells are generally considered to be more sensitive to contrasts of high spatial frequency, a decrease in the number of these cells might produce poorer acuity. However, Chino, Shansky, and Hamasaki (1977) reported that there was a decrease of Ycells in Siamese cats compared to normal cats.

Hubel and Wiesel (1971) speculated that the visual capabilities of the Siamese cat may be decreased due to the complex input at the cortical level. While the aberrant projections of the Siamese cat are certainly sufficient to disrupt binocularity, it does not seem necessary that poor acuity would result. It is known that binocular acuity is greater than monocular acuity, but the differences are not sufficient to account for the findings of this study (Campbell and Green, 1965).

Other factors which remain as possible causes are optical blurring of the image. This seems unlikely, since there seemed to be no gross difference ophthalmoscopically between the Siamese and normal cats tested. Additionally, optical blur would produce only a high frequency depression of contrast sensitivity, not a low frequency depression as seen in the data of this study and Blake and Antoinetti (1976). However, until this possibility is tested, it must be considered.

Perhaps the lack of retinal pigmentation in Siamese cats causes increased light scattering. This could cause decreased acuity and contrast sensitivity.

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It is known that the severity of the geniculate anomaly in mink is related to the amount of retinal pigmentation (Sanderson, et al., 1974).

Creel, Whitkop and King (1974) have found evidence in humans that indicates abnormal retinal projections in humans may be associated with retinal hypopigmentation. They found decreased ipsilateral evoked potentials compared to contralateral evoked potentials in 14 of 20 human albinos, whose albinism resulted from a variety of causes. They found no difference between ipsilateral and contralateral evoked potentials in normally pigmented subjects. Perhaps acuity is related to the amount of retinal pigmentation. This warrants further study.

The spatial properties of single units also need investigation. There is good evidence showing that the highest spatial frequency to which single neurons can respond has correlation with behavioral and psychophysical acuity (Enroth-Cugell and Robson, 1966; Campbell, Cooper and Enroth-Cugell, 1969; Maffei and Fiorentini, 1973; Cleland, Dubin, and Levick, 1971). Perhaps the single units of the Siamese cats will respond only to spatial frequencies of lower value than normal cats. Chino, Shansky and Hamasaki (1977) lend support to this hypothesis. They reported that the retinal ganglion cells of the Siamese cats from which they recorded were less responsive to contrast than were the cells from normal cats.

Perhaps the poor acuity of the Siamese cat is due to inhibition. From the data of Guillery and Casagrande (1975b), it appears there may be inhibition of ipsilateral eye input by the contralateral eye. This might cause decreased visual acuity. The question of an active inhibitory process needs investigation. Several methods of investigating this have been and are

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now being used in several laboratories to study visual deprivation. These methods should be tried with Siamese cats to discover if the ipsilateral eye input is being inhibited by the contralateral eye.

This study has demonstrated that the visual function of the Siamese cat is poorer than the normal cat. There appear to be three possible explanations for this, none of which is exclusionary of the others. The decreased visual function may be due to light scattering resulting from decreased retinal pigmentation, single units which do not respond to high spatial frequencies, active inhibition of the ipsilateral eye by the contralateral eye, or any combination of the above. Further experiments will have to reveal the actual cause of the decreased acuity of the Siamese cat.

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