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VISUAL DISCRIMINATIONS DURING EYELID CLOSURE IN THE CAT

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SUMMARY

We were able to train cats raised with sutured eyelids to perform simple brightness discriminations before their lids were parted. If, and only if, a small hole was present in a lid, could some of the cats also perform a grating orientation discrimination.

By establishing their thresholds for the brightness discrimination before and after dark adaptation and before and after the lids were opened, we reached three main conclusions. (1) During dark adaptation (with pupils maximally dilated and retinae most sensitive, regardless of lid suture), the cats were 3–4 log units more sensitive with the lids open than with the lids closed. This indicates a 3–4 log unit attenuation for the lids which is in agreement with our photometric measurements. (2) During light adaptation, the sensitivity difference between the conditions of opened and closed lids was only 1–2 log units. We concluded that factors (such as pupil dilatation and retinal sensitivity) partially compensated for the lid attenuation, since the open eye could have a smaller pupil and less sensitive retina during light adaptation. (3) Given these potential compensatory features of the pupil and assuming consensual pupil sizes, the deprived eye of a monocularly sutured cat may suffer more photic deprivation (since the pupil behind the closed lid would be as constricted as the pupil in the open eye) than would either eye of a binocularly sutured cat (where both pupils can be relatively large).

INTRODUCTION

A great deal of current research has been directed at an analysis of the effects of early visual deprivation upon the developing mammalian visual system. A common

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experimental subject has been the visually deprived cat in which deprivation is produced by eyelid suture[19]. This procedure deprives developing visual system structures of normal light and pattern stimuli and causes a variety of anatomical[11,19], physiological[3,18–21], and behavioral[7,15,16] abnormalities.

The extent of recovery from these effects is an issue of current debate, with some laboratories claiming little or no recovery[7,16,21] and others claiming substantial recovery[4]. While anatomical and physiological data have been gathered over the entire postdeprivation period, little information is available regarding the visual perception or behavior of these animals immediately following eyelid opening, since by all accounts a cat behaves as if it is blind for a period of time varying from hours[15,16] to months[8] following eyelid opening.

In an attempt to provide behavioral data at the earliest possible point following eyelid opening, we trained several binocularly and monocularly lid-sutured cats, before their eyes were opened, to make the basic motor responses required in a simultaneous two-choice discrimination apparatus[1]. We began a series of experiments to explore the visual discrimination abilities of these animals while their eyelids were still closed.

The first questions asked were: (1) can a lid-sutured cat respond to any light stimulus while still deprived (i.e., can the cat 'see' before and/or immediately after the eyes are opened), and (2) what are the psychophysical boundaries of those visual abilities which exist during eyelid closure? Furthermore, we have attempted to assess the perceptual consequences of the small holes sometime present along the suture scar of a deprived eye. We did this by testing several lid-sutured cats with and without small lid holes.

METHODS

Subjects

Five binocularly deprived cats (BD28, BD36, BD46, BD47, BD48) and one monocularly deprived cat (MD13), ranging in age from 10 to 21 months, were selected from the colony. These cats were born and raised in the laboratory. They were individually housed, with a 12 h light period and free access to water. Each cat was reduced to 80% of its free feeding weight and maintained at that level of food deprivation throughout the testing period. All animals had undergone eyelid suture at or before 10 days of age, and lid closure was rigorously maintained throughout the first 6 months of age. At the onset of this study, however, a small opening (0.5–1.0 mm) was apparent upon close inspection in one lid of each of 3 of the cats (BD36, BD46, BD48). These openings were all central in the lids (i.e., over the corneas). Three other cats had complete lid closures (BD28, BD47, MD13).

Apparatus

The behavioral procedures were essentially those of Berkley[1]. The discrimination apparatus was an operant conditioning box with a head chamber located at one end into which the cat thrust its head. The head chamber contained two clear plastic response keys, 1.5 cm behind which were located two small projectors (BRS/LVE 111-06). These projectors presented the desired stimuli upon two translucent viewing screens visible through the response keys. Between and below the response keys, as a reward, a small squirt of diluted beef baby food was delivered from a solenoid feeder through a small hole in the head chamber.

Two visual discrimination problems were utilized: 'light' versus 'dark' (1.5 cm × 1.5 cm squares, 'light' luminance 36.3 cd/sq.m versus 'dark' luminance 1.1 cd/sq.m) and horizontal versus vertical stripes (two cycles of a square wave grating, 0.1 cycles/degree at response distance, 93% contrast, space average luminance 18.5 cd/sq.m).

Stimulus values were determined periodically with both a Tektronix J16 Digital Photometer (J6502 probe) and an SEI photometer. All experimental contingencies and data acquisition were accomplished with electromechanical equipment.

Training

All 5 binocularly deprived cats were trained with both eyes still closed. MD13 was trained with an opaque black plastic contact lens over its non-deprived eye. This lens completely covered the cornea and remained in place during all testing.

Each cat was trained to press the response keys with its nose by a method of successive approximation. Paw responses were eliminated by adjusting the diameter of the entrance to the head chamber. The light/dark stimuli were present during shaping (room lights on), although each of the initial 30 responses were reinforced. The day following response acquisition, discrimination training was begun with room lights off. Each cat was given 125 trials/day, 5–7 days/week. A response to the correct key was immediately reinforced and was followed by a longer intertrial interval, which was initially 3 sec but gradually increased to a maximum of 12 sec. Responses during the intertrial interval reset the interval to the duration of the incorrect interval. The position of the correct stimulus was determined by a Gellerman series in conjunction with an intertrial correction procedure under which only correct responses advanced the sequence to its next position. If an error occurred, the stimuli remained in the same positions as on the previous trial. This correction procedure is a powerful deterrent to the cats' initial and recurrent tendency to respond predominantly to one key. Criterion performance was taken as four consecutive days of 80–89% correct ($P < 10^{-6}$) or two consecutive days of 90–100% correct ($P < 10^{-5}$).

Each cat was first trained to criterion on the intensity discrimination with either light or dark correct. After achieving criterion on this problem, the cats were trained on the stripe orientation discrimination. Training continued to criterion or until 30 sessions had been completed with performance at chance levels.

Threshold testing

Following the initial intensity and orientation discrimination training, two cats, BD36 and MD13, were tested for their intensity discrimination thresholds under conditions of light and dark adaptation. They were tested this way both with their eyelids closed and opened. This was done in order to estimate the functional density of the cats' eyelids by comparing their intensity discrimination thresholds before and after lid opening (BD36) or separately through a deprived eye and non-deprived eye in the same cat (MD13).

Psychophysical testing was conducted as follows. Both cats were tested on the light/dark discrimination with a 3 sec intertrial interval and no correction procedure. A light adapted frequency-of-seeing function was determined for BD36 and MD13 by inserting Kodak neutral tint filters in the light path of both projectors. During a daily test session of 200 trials, the cat responded for 50 consecutive trials at one stimulus intensity. This was followed by 50 consecutive trials at a different stimulus intensity, etc. The sequence of intensities for these 50 consecutive trials was randomized within and between the daily sessions. This procedure was followed for 4 consecutive days so that 200 trials were performed at each of the 4 stimulus intensities. During the light adapted threshold determinations, the cat was taken from the fluorescently illuminated (20.6 cd/sq.m) colony room and tested with the room lights on. Ambient illumination in the head chamber was 10.3 cd/sq.m. MD13 was tested first with its open (non-deprived) eye and then with its deprived eye by placing the opaque black plastic contact lens over the non-deprived eye. BD36 was tested in a similar manner with both eyes closed.

A dark adapted probability-of-seeing function was then determined by first dark adapting each cat for at least 60 min (see ref. 14) in a double-walled black box, then the cat was tested in a dark room with the stimuli being the only source of illumination. Due to the inconvenience of changing the neutral tint filters in the dark, each cat was tested for 125 trials/day at one stimulus intensity. Each stimulus intensity was tested on two days and the sequence of intensities across days was random. MD13 was first tested with its non-deprived eye and then with its deprived eye as outlined above. BD36 was tested with both eyes closed.

Subsequent to the determination of the light and dark adapted probability-of-seeing functions, BD36 was anesthetized and lids opened for the first time. Over the next 10 days, light and dark adapted probability-of-seeing functions were determined for BD36 with its eyes open. Following this the lids of BD36 were again sutured closed and a final dark adapted probability-of-seeing function was determined.

Photometric measurements

In order to provide more detailed measurements of the density of the cats' eyelids over a range of ages, we measured the light attenuation of freshly excised lids as a function of wavelength in several young and adult cats (cf. ref. 5). The cats were anesthetized and studied in another, terminal experiment. The lids were excised, dried gently with facial tissue, and studied within one hour. No hair was removed. Photometric measurements were made through portions of the lids not including the midline scar. No detectable change in lid density occurred during the measurements, and storage in cold saline overnight produced no detectable change in optical density. For the measurements, the lid was placed across a 5 mm aperture over the J-6502 probe of a Tektronix J16 Digital Photometer. A tungsten light source was used to focus a 6 mm spot of light (1060 μW/sq.cm) upon a linear wavelength wedge (2.2 nm/mm, half width 11–12 nm, Jenaer Glaswirk Schott and Gen., Mainz) so that the light incident upon the eyelid encompassed approximately 24 nm. Intensity measurements were made from 400 to 700 nm every 30 nm with and without the eyelid over the probe. Transmittance was determined by dividing the illuminance through the lid by the illuminance without the lid at each wavelength step.

RESULTS

Behavioral results

Fig. 1 presents the discrimination performance of one BD cat (BD36) which had a small lid hole in one eye and one BD cat (BD28) which had no lid holes. As can be seen, BD36 achieved criterion on the light/dark discrimination immediately and required 7 sessions to reach criterion performance on the horizontal/vertical discrimination. At this point the small hole was closed and the cat retested on both discriminations. Again light/dark was easily discriminated but the horizontal/vertical discrimination was abolished. BD28 was trained to discriminate dark/light within 35 sessions but remained at chance levels on the horizontal/vertical discrimination after 30 sessions. These two cats were representative of their lid condition groups in that all 3 cats with lid holes reached criterion performance on both discriminations, while those cats without lid holes were capable of discriminating light/dark but not stripe orientation. Table I summarizes these data. Following this initial discrimination, BD36 (whose initial lid hole healed closed) and MD13 were tested for light and dark adapted intensity discrimination thresholds.

The results of these procedures are presented in Fig. 2. A frequency-of-seeing

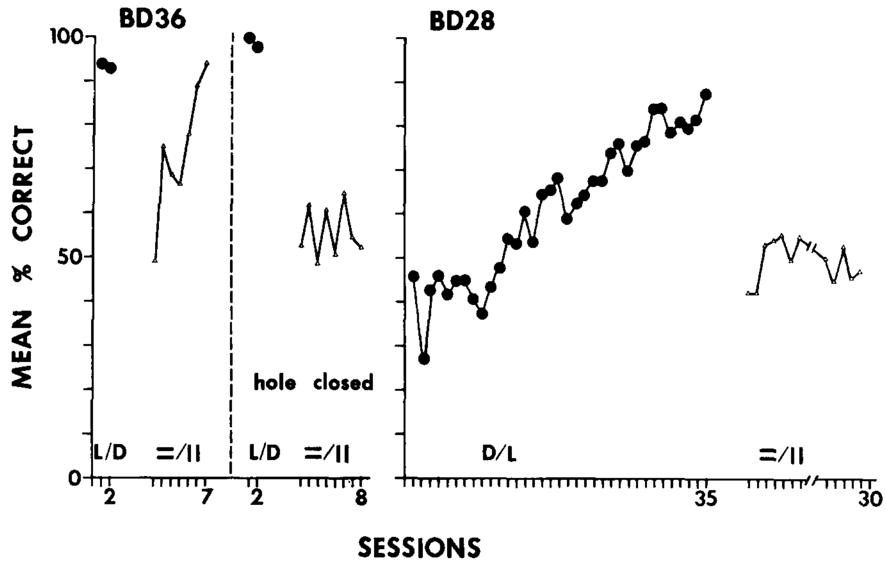

Fig. 1. Initial learning curves for an intensity discrimination (small open triangles) and a stripe orientation (large filled circles) for BD36 and BD28. For both cats, the positive stripe orientation was horizontal; on the intensity problem, BD36 was taught to chose the brighter stimulus, and BD28, the darker one. BD36 had a small lid opening over one cornea (< 1 mm diameter) during initial learning; re-testing followed complete lid closure. BD28 never had such a detectable lid opening.

TABLE I

Sessions to criterion for deprived cats with or without lid holes on a light/dark and stripe orientation discrimination

The positive stimulus is indicated in parentheses (i.e., L for light, D for dark, H for horizontal stripes, and V for vertical stripes). The asterisks indicate that after 30 sessions, performance failed to exceed chance levels.

	Light/dark	*Stripe orientation*
Lid holes		
BD36	2(L)	7(H), 30(H)*
BD46	6(L)	9(V)
BD48	5(L)	31(H)
No lid holes		
BD28	35(D)	30(H)*
BD47	4(L)	30(V)*
MD13	16(L)	30(H)*

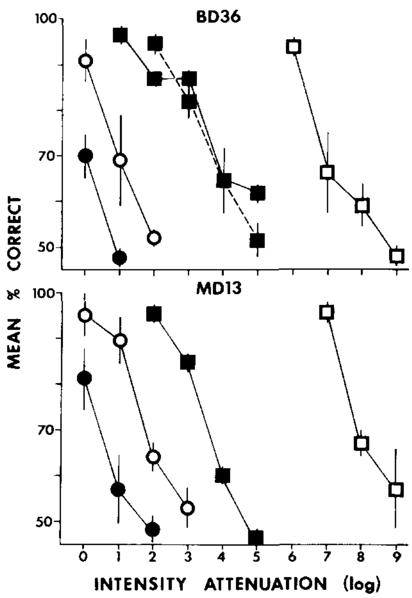

Fig. 2. Psychophysical testing to estimate the visual thresholds of a brightness discrimination for a binocularly deprived cat (BD36, upper graph) and a monocularly deprived cat (MD13, lower graph). Circles represent testing with room lights on (i.e., partial light adaptation) and squares represent testing with room lights off after one hour of dark adaptation. Each symbol represents the performance on 200–250 trials in blocks of 50, and the vertical lines represent the standard errors for these averages. For BD36, filled symbols represent testing with the lids closed, and open symbols, with the lids open; the filled squares connected by the dashed line represent re-testing after re-closing the lids. For MD13, filled symbols represent testing of the closed, deprived eye with an opaque occluder covering the non-deprived eye, and open symbols represent testing of the open, non-deprived eye with occlusion of the deprived eye. With 70% mean correct taken as the threshold value, BD36 had its threshold raised by 0.9 log units due to eyelid closure during partial light adaptation and by 3.1 log units after dark adaptation. These values for MD13 were 1.3 log units during partial light adaptation and by 4.3 log units after dark adaptation (see text).

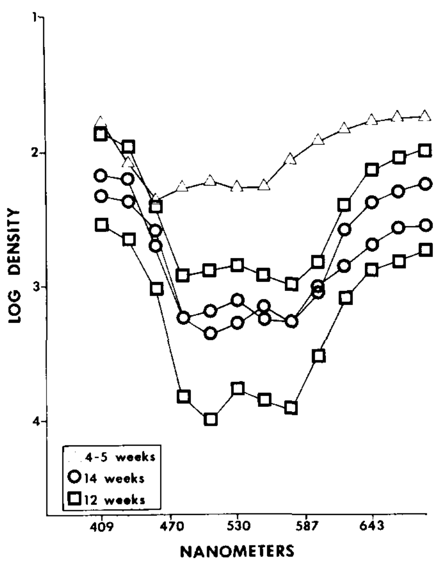

Fig. 3. Optical density (energy through lid divided by incident energy) as a function of wavelength for the lids of 3 kittens. Only one lid from the youngest kitten was measured, but both from the other two kittens were measured. Data from adult cats are not illustrated because they are indistinguishable from those shown for the 12- and 14-week-old kitten.

function was constructed for each of the 4 conditions for both cats by plotting the cats' performance levels (mean per cent correct) at each stimulus intensity. Each data point was determined by 200–250 trials. Threshold discrimination was arbitrarily defined as that stimulus intensity corresponding to the 70% correct performance level as estimated from the frequency-of-seeing functions.

It is apparent for both cats that the level of discrimination performance with the deprived eye(s) still sutured closed was a monotonic function of the stimulus intensity. Furthermore, dark adaptation made both cats' frequency-of-seeing functions 3–4 log units more sensitive, further establishing that the stimulus light was controlling the animal's performances. As was expected, BD36 was more sensitive with eyes open under both light and dark adapted conditions. During light adapted testing, the sensitivity of BD36 increased from a threshold (70% correct) of 0.0 log I attenuation with its eyes closed to a sensitivity of 0.9 log I attenuation with its eyes open. During dark adapted testing the threshold of BD36 with eyes closed was 3.8 and 3.7 log I attenuation and increased to 6.85 log I attenuation with eyes open.

Similar results were obtained with MD13. Under light adapted testing, the sensitivity of MD13 with the closed eye was 0.4 log I attenuation and 1.7 log I attenuation with the open eye. Following dark adaptation its threshold with the closed eye was 3.6 log I attenuation and 7.9 log I attenuation with the open eye. This 7.9 log unit difference corresponds to an absolute threshold of 4×10^{-7} cd/sq.m. for the cat with its non-deprived eye, and this is in excellent agreement with previous measurements of cat absolute thresholds (see Table I, p. 69, of ref. 2).

Photometric results

The results of the physical measurements of lid density are presented in Fig. 3. The cat's eyelid appears to have its maximum density to wavelengths between 470 and 570 nm, transmitting more incident quanta at longer and shorter wavelengths. Maximum density also appears to increase from 2 log units in a 4–5 week-old kitten to 3–4 log units in a 12- or 14-week-old kitten.

The lids of several adults were measured, and these values also fell between 3 and 4 log units. There was substantial inter- and intra-cat variability in that the 12-week-old kitten's right and left eyelids differed by a full log unit, and the difference between one lid of the 12-week-old kitten and both-lids of the 14-week-old kitten was also approximately one log unit.

DISCUSSION

The results of these experiments point to several important aspects of the perceptual consequences of visual deprivation by eyelid suture in the cat. The first and most obvious conclusion is that a visually deprived cat is not blind for any period of time following eyelid opening, since the cat is not blind before the lids are opened. All three deprived cats (BD28, BD47, MD13) having complete lid closure from birth acquired the light/dark discrimination at a rate within normal bounds. In fact, BD36 performed at criterion levels within the first 125 trials (see Fig. 1), and we have never seen such rapid learning in normal cats. This could result from a stronger positive phototaxis for deprived than for normal cats. A second important finding of the discrimination testing was that any small lid opening overlying the cornea provided sufficient vision to enable the cat to perform the stripe orientation discrimination, and it should be emphasized that several of these incomplete lid closures were not apparent without the closest scrutiny. Although the possibility exists that these cats based their discriminations upon the presence or absence of light at some selected portion of the stimulus, this nevertheless indicates a degree of spatial vision not present under conditions of complete lid closure. Presumably these small holes act like artificial pupils. The influence of these small lid holes has not been systematically analyzed anatomically or physiologically and may form the basis of some of the current discrepancies regarding the effects of deprivation.

Optical density of the lids

Wiesel and Hubel[19] estimated with photometric techniques that the cat's eyelid attenuates light by 4–5 log units. Recently, Crawford and Marc[5], also using photometry, found the attenuation to be only 1–2 log units depending upon wavelength. Our photometric data provide an intermediate estimate, namely, that the eyelids of an adult cat attenuate incident illumination by 3–4 log units through a wavelength range encompassing the λ max. of the cat's scotopic and photopic spectral sensitivity[6,14]. These different estimates could result from the substantial variability among cats in terms of lid transmittance (see our Fig. 3 and ref. 5) and/or subtle differences in technique. For instance, Crawford and Marc[5] measured transmittance in situ which should provide a more relevant measure, but they stretched the lids over the probe and removed the hair from the lid, both of which, they pointed out, could have caused artificially high transmittance readings.

Because of these ambiguities, we believe that our behavioral data might provide a more reliable estimate of lid attenuation (see Fig. 2). The ability of a cat to detect a light stimulus depends on a number of factors, including pupil size and retinal sensitivity (i.e., the level of dark adaptation). Therefore, to control for these variables between cats tested with open and closed eyes, we studied them after extensive dark adaptation. This procedure presumably equated pupil size (to a maximum aperture) and the retinae should have been equally and maximally dark adapted. Thus the dark adapted data for BD36 and MD13 (Fig. 2), which compare thresholds in the dark adapted state between opened and closed eyes, provide a measure of lid attenuation. Interestingly, the attenuation value thus derived is 3–4 log units, which is in good agreement with our photometric estimate.

Implications for deprivation by lid suture

A major question of interest is: to what extent does neonatal lid suture create photic deprivation of the visual system? Two points must be considered. First, the cat's visual system is sensitive to the effects of lid suture only during an early critical period of the first few postnatal months[12]. Fig. 3 indicates that lids of younger cats attenuate light less than those of adult cats (i.e., total attenuation may be only about 2 log units during the critical period). Therefore, the measurements from adult animals in this and other studies[5,19] probably overestimate the effectiveness of the lids to attenuate light.

Second, these photometric measurements estimate the amount of light striking the *cornea* through the lids, but a much more salient measure in terms of visual deprivation is the amount of light striking the *retina*. A major factor in this consideration is pupillary area. According to Berkley (Table VIa, p. 110 of ref. 2), the cat's pupil is capable of more than a 2 log unit change in area. Pupil size varies apparently in order to clamp the retinal illumination at mesopic levels[2,14]. Since, in the light intensity of our housing facility, the cats normally have partially constricted pupils, we must consider the possibility that with lid suture, the pupils enlarge to compensate at least partially for decreased light intensity at the cornea. That is, retinal illumination of lid-sutured cats is probably much closer to that of normal cats than would be predicted from only a consideration of lid attenuation. In fact the data from Fig. 2 support this view. When partially light adapted, MD13 and BD36 with open eyes and partially constricted pupils had thresholds only about one log unit less than they had with closed eyes. Since these same cats provided the behavioral estimate that lid attenuation was 3–4 log units (i.e., after dark adaptation; see above), some factor is compensating for about 2–3 log units of the lid's attenuation. A likely explanation for at least part of this phenomenon is increased pupillary dilatation after eyelid closure, although other factors, such as increased retinal sensitivity, might also play a role. Given both the relatively high transmittance of a kitten's lid (i.e., during the critical period) and also the potential compensation of lid attenuation by the pupil, it is possible that photic deprivation at the retina may be minimal in lid-sutured cats.

One final point must be considered. Pupillary reactions are probably consensual in lid-sutured cats, as they are in normals. Given this assumption, it is then probable that binocular lid suture results in relatively large pupils in both eyes and relatively little photic deprivation of the retina. If only one eye is closed, pupillary sizes are probably controlled by the functional, non-deprived eye, and the size of the non-deprived pupil appears roughly equal to those of normal cats (i.e., partially constricted in our cat colony environment). With consensual pupils, the deprived eye now has a smaller pupil (and more retinal photic deprivation) than each eye of a binocularly deprived cat would have. This may in part explain some of the differential effects of monocular versus binocular suture. One example is cell size in the lateral geniculate nucleus. The deprived cells after monocular suture are much smaller than those after binocular suture, the latter being practically normal[10,11]. Interestingly, Kalil[13] has recently reported that total dark rearing results in very small geniculate neurons. While these data are consistent with the idea that the level of photic energy at the retina might control development of geniculate cell sizes (and other developmental properties), they do not explain how the monocular segment (i.e., peripherally represented portions) of the lateral geniculate nucleus escapes these and other consequences of monocular deprivation[9,11,17,18].

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