Eye Movements Initiate Visual-Motor Development in the Cat

Abstract. *Visually naïve kittens turn their eyes toward visual targets but lack other visual-motor coordinations. Light-reared animals were able to mediate guided behaviors with an immobilized eye, but animals with the eye immobilized before initial exposure to a lighted environment were not. Eye movement is implied to play an essential role in visual-motor development.*

Upon first being brought into light, visually naïve kittens turn their eyes toward high-contrast visual targets but lack other visual-motor coordinations. The animals cannot move about so as to avoid colliding with objects, they do not refrain from walking off edges, and they are unable to reach with the forelimb to contact visual targets (*1*). We now report that when eye movements are prevented, these other capacities do not develop.

Previous studies have shown that the behaviors absent in visually naïve kittens are acquired if the conditions of exposure in light (that is, to a lighted environment) permit changes in visual input to be systematically related to self-produced movement. The developmental process was described as the formation of a representation of visual space, which incorporates information contained in various motor-visual feedback loops. Manipulating exposure conditions permitted the feedback required for acquisition of each of several components of visually guided behavior to be identified (*2*). For example, the ability to guide the entire body with respect to the location of objects was acquired if and only if displacement of images upon the retinas was systematically associated with locomotion. That kittens permitted to move about in light only under stroboscopic illumination failed to develop visually guided behaviors reveals the essential contribution made by motion of contours across the retinas (*3*).

Images are displaced on the retinas when the eyes move. Because fixation responses are present soon after birth, they provide frequent and reliable early opportunity to correlate motor commands with their visual consequences. We speculated that eye movements might be primary developmentally as well as historically; eliminating the capacity to fixate targets (and the visual feedback that would result from fixation) might preclude utilizing subsequent feedback opportunities. Our experiments indicate that surgical immobilization of the eye does prevent the acquisition of visually coordinated behavior. An immobilized eye is capable, however, of mediating guided behaviors that had been acquired prior to the surgery. These results are interpreted as indicating that feedback from visually elicited eye movements is essential to the construction of a representation of visual space.

The method used to immobilize the eye of a kitten was unilateral denervation of the extraocular muscles by sectioning cranial nerves III, IV, and VI. The nerves were exposed by incising the soft palate and removing part of the sphenoid bone lateral to the optic nerve. Cranial nerves III, IV, and VI were gently dissected from nerve V and sectioned just caudal to the orbit (*4*). Two groups of dark-reared kittens were operated on at 6 to 8 weeks of age. The first group comprised four animals (animals 1 to 4) in which the eye contralateral to the denervated eye was sutured shut. These kittens were kept in light continuously after the surgery. The other group comprised six animals (animals 5 to 10) in which the contralateral eye was left open. These kittens were kept in the dark after surgery except for 3 hours of daily monocular exposure to light with each eye exposed on alternate days.

None of the kittens were able to move the immobilized eye toward high-contrast visual targets. The absence of postrotatory nystagmus of that eye, which is consistent with paralysis, was also confirmed repeatedly. Formal testing of visually guided behavior began after the kittens had been provided 2 weeks of exposure in light. In intact animals of this age, all visually guided responses are observed after a much shorter period in light (*5*). The kittens in which only the immobilized eye had been exposed displayed visually triggered extension of the forelimb when they were lowered slowly toward a broad horizontal surface. They could not reach accurately toward visual targets, though, and, in formal testing, they failed to guide the forelimb across a gap to the position of a movable bridge (Table 1). In an obstacle course they repeatedly collided with objects and showed frequent startle responses (*6*). Both visually guided reaching and visually guided locomotion were reexamined periodically. When the experiment was terminated a year later, neither capacity had been acquired. This result is consistent with the hypothesis that the absence of visually elicited eye movements precludes developing visually guided behavior.

When tested while using the immobilized eye, the kittens that had been provided alternating monocular exposure to light after unilateral cranial nerve section were indistinguishable from the group in which only the immobilized eye had been exposed (Table 1). When tested with the intact eye (after 21 hours of exposure of that eye), they displayed both visually guided locomotion and reaching (Table 1). Thus, the failure to mediate these behaviors with the immobilized eye was not due to some general disruptive or inhibitory effect of the surgery. In addition, eliciting a consensual pupillary response in the intact eye to changes in illumination of the immobilized eye provided evidence that input to the denervated eye was being processed.

A number of questions arose in interpreting these data. Sectioning cranial nerve III paralyzes the intraocular muscles serving accommodative and pupillary reflexes. Resulting degradation of the retinal image might contribute to the failure to acquire visually guided behaviors. It is possible to paralyze the intraocular muscles without eliminating eye

Table 1. Visually guided reaching after different experimental treatments. Eight trials were given each cat with the bridge positioned randomly to the animal's right or left. Interspersed crossings with the bridge directly ahead helped maintain the behavior.

Condition of exposure in light	Cat	Reaches (hits/misses)	
Immobilized eye alone	1	0/8	
	2	0/8	
	3	0/8	
	4	1/7	
Immobilized and intact eye exposed alternately	5	2/6	8/0*
	6	0/8	8/0*
	7	2/6	7/1*
	8	2/6	8/0*
	9	0/8	8/0*
	10	1/7	7/1*
With atropine	11	7/1	
	12	8/0	
	13	8/0	
After vestibulectomy	14	8/0	
	15	7/1	
	16	7/1	
Binocular preoperatively	17	8/0	
	18	7/1	
	19	8/0	
Binocular postoperatively	20	8/0	
	21	7/1	
	22	7/1	

*Intact eye.

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movement by applying atropine topically. To evaluate the contribution of this factor, a new group of three dark-reared kittens (animals 11 to 13) 6 to 8 weeks of age had one eye sutured shut and the contralateral eye left intact. These animals remained in the dark except for 3 hours of daily exposure in light. Ophthalmic atropine (1 percent) was applied each day 20 minutes before the animals were removed from the dark and reapplied immediately before exposure. The pupil of the eye remained fully dilated during the entire period in light. After 1 week, at the end of the daily exposure period, the kittens were tested for visually guided locomotion in the obstacle course and visually guided reaching to the bridge. Both capacities were present. After another week of exposure with atropine applied to the eye, retesting indicated that the behaviors remained intact (Table 1). Thus, the absence of accommodative and pupillary reflexes did not prevent the kittens from acquiring visually guided behaviors during 1 week of exposure in light and did not degrade those behaviors during an additional week of exposure. Therefore, the failure of kittens to exhibit guided behaviors after cranial nerve section cannot be attributed to their lacking these reflexes.

Denervating the extraocular muscles precludes the elicitation of eye movements by vestibular as well as visual input. Eliminating the vestibulo-ocular reflex might result in sufficient blurring of the retinal image to interfere with the extraction of information from motor-visual feedback. To determine the developmental consequences of eliminating the vestibulo-ocular reflex, a new group of three dark-reared kittens (animals 14 to 16) 6 weeks of age was subjected to bilateral vestibulectomy. The vestibular apparatus was approached ventrally through the acoustic bullae, and the petrous portion of the petromastoid bone was excised. After surgery, the animals were kept in light continuously and examined repeatedly for evidence of postrotatory nystagmus. This response remained permanently absent, indicating that the vestibular apparatus was no longer functioning.

Initially, the vestibulectomized kittens were both ataxic and hyperactive. Three months after surgery, these problems had subsided sufficiently for us to test visually guided behaviors. At this time the animals traversed the obstacle course without colliding with objects and reached accurately with the forelimb to the position of the bridge (Table 1). Acquiring these responses in the absence of vestibular input implies that the interference with visual-motor development consequent on eye immobilization is not due to eliminating the vestibulo-ocular reflex.

It remained possible that some unknown effect of denervation surgery prevented the animal from responding to visual input to the immobilized eye. The display of a consensual pupillary response of the intact eye to changes in illumination of the immobilized eye, along with the capacity of the denervated eye to mediate visually triggered extension of the forelimb, made this unlikely. Moreover, if, as we have suggested, the contribution of eye movement to visual-motor coordination is made during the formation of a representation of visual space, guided behaviors acquired before eye immobilization might be spared after denervation. This result would also show that the surgery per se does not preclude guidance.

To explore this possibility, three light-reared kittens (animals 17 to 19) 6 to 8 weeks of age were tested while using only one eye. The presence of visually guided locomotion and visually guided reaching was confirmed. Subsequently, the tested eye was immobilized by unilateral section of cranial nerves III, IV, and VI. After the animals recovered from surgery, guided behaviors were mediated by the immobilized eye (Table 1). Thus, denervation of the ocular muscles did not prevent the eye from controlling visually guided behaviors. This outcome is consistent with the readily made observation that eye movements need not occur during the execution of visually guided behaviors. The contrasting effects of eye immobilization in animals reared preoperatively in dark and light specify that it is in the initial acquisition of those behaviors that eye movements play a critical role.

The light-reared kittens subjected to cranial nerve section differed from the visually naive kittens so treated in two respects. First, they had already acquired visually guided behaviors. Second, they had acquired those behaviors under conditions of binocular exposure in light. A series of studies is underway to segregate these factors. When intact kittens are exposed in light under conditions differing for each eye, behaviors acquired under the control of one eye are not mediated by the other (*7*). This result suggests that for the light-reared animals of the present study, their binocularity during preoperative exposure may have been crucial to the subsequent display of behaviors guided by the immobilized eye. Results obtained with three kittens (animals 20 to 22) indicate that binocular exposure after unilateral cranial nerve section supports mediation of guided behaviors by the immobilized eye (Table 1). A complementary result would be a failure of animals provided alternating monocular exposure before unilateral denervation to mediate guided behaviors with the immobilized eye. The experiments reported here support the hypothesis that eye movements are essential to the formation of a representation of visual space; the conditions under which an immobilized eye has access to this representation remain to be determined.

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References and Notes

1. The ocular fixation reflex has been studied in the unanesthetized pretrigeminal cat by B. Dreher and B. Zernicki [*Acta Biol. Exp. (Warsaw)* **29**, 359 (1969)] and is also readily observed in intact kittens, along with optokinetic nystagmus [for example, F. Vital-Durand, P. T. S. Putkonen, M. Jeannerod, *Vision Res.* **14**, 141 (1974)]. Deficiencies following dark-rearing have been described by A. H. Riesen [in *Biological and Biochemical Bases of Behavior*, H. F. Harlow and C. N. Woolsey, Eds. (Univ. of Wisconsin Press, Madison, 1958)], R. D. Walk and E. Gibson [*Psychol. Monogr.* **75** (No. 15) (1961)], and J. Warkentin and K. U. Smith [*J. Genet. Psychol.* **50**, 371 (1937)].
2. R. Held and A. Hein [*J. Comp. Physiol. Psychol.* **56**, 872 (1963)] showed that systematic feedback from self-produced movement was essential to acquiring visually guided locomotion. Studies specifying the relation between exposure conditions and development have been summarized by A. Hein and R. Diamond [*ibid.* **81**, 394 (1972)].
3. A. Hein, R. Held, E. Gower, *ibid.* **73**, 181 (1970).
4. Sparing cranial nerve V preserves the afference believed essential to elicit blinking, thus preventing possible dessication and eventual clouding of the cornea. This procedure was used in the monkey by F. Koerner and P. Schiller [*Exp. Brain Res.* **14**, 318 (1972)] and was described fully for adult cats by P. Wilkerson [thesis, University of North Carolina at Greensboro (1978)].
5. A. H. Riesen, *J. Nerv. Ment. Dis.* **132**, 21 (1961).
6. Details of procedures for testing visually guided reaching and visually guided locomotion have been given by A. Hein and R. Diamond [*J. Comp. Physiol. Psychol.* **76**, 31 (1971)].
7. For example, when a kitten moves about in a normal laboratory environment with the view of one of the forelimbs provided by only one eye, guided reaching with that limb is mediated only by that eye [A. Hein and R. Diamond, *ibid.*, p. 219].
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