

Visuomotor Adaptation to Displacing Prisms by Adult and Baby Barn Owls

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The capacity of barn owls to adapt visuomotor behavior in response to prism-induced displacement of the visual field was tested in babies and adults. Matched, binocular Fresnel prisms, which displaced the visual field 11°, 23°, or 34° to the right, were placed on owls for periods of up to 99 d. Seven baby owls wore the prisms from the day the eyelids first opened; 2 owls wore them as adults. Prism adaptation was measured by the accuracy with which a target was approached and struck with the talons, a behavior similar to pointing behavior used commonly to assess prism adaptation in primates.

Baby and adult owls exhibited a limited capacity to adapt this visuomotor behavior. Acquisition of adapted behavior was slow, taking place over a period of weeks, and was never complete even for owls that were raised viewing the world through relatively weak (11°) displacing prisms. When the prisms were removed from adapted owls, they struck to the opposite side of the target. The recovery of strike accuracy following prism removal was rapid; 7 of 9 owls recovered normal accuracy within 30 min of prism removal, despite having worn the prisms for months. This limited capacity for adaptation contrasts dramatically with the extensive and rapid adaptation exhibited by adult primates exposed to comparable prismatic displacements.

The mechanism of adaptation used by the owls was to alter the movements employed for approaching targets. Instead of moving straight ahead, the head and body moved diagonally relative to the orientation of the head. Thus, in contrast to prism adaptation by humans that can involve reinterpretation of eye, head, and limb position, prism adaptation by owls is based on changes in the motor commands that underlie approach behavior.

Approaching an object is a complex visuomotor task requiring the integration of information from a variety of sources. First, the position of the object's image on the retinae must be interpreted. Second, the direction of gaze, i.e., the position of the eyes in the head and of the head on the body, must be accounted for so that the perception of the object's location remains stationary as the eyes and head move. Third, the positions of the

limbs must be evaluated in order to determine what movement would be appropriate. If this information is analyzed correctly, motor commands can generate movements that bring the animal to the desired object, but only if the motor commands themselves are properly calibrated. Error in any one of these processes will cause an animal to approach objects inaccurately, interfering with the animal's vital abilities to acquire food and interact with the environment.

A feedback signal that the brain could use to evaluate the performance of these processes is the stability of an object's image on the retinae as the object is approached. An inaccurate approach causes the image of the object to move across the retinae in a direction opposite to the direction of error. This feedback signal, which is analogous to the retinal slip signals used to calibrate the vestibulo-ocular reflex for stabilizing the eyes during head movements (for reviews see Melvill-Jones, 1977; Miles and Lisberger, 1981) and to calibrate smooth pursuit eye movements for tracking moving objects (Heywood and Churcher, 1971; Pola and Wyatt, 1980), could be used to adjust the perception of object location and the movements necessary to approach desired locations.

Does the brain use visual feedback to adjust these processes? If so, are adjustments made at one or at several stages in the computation of approach behavior? Are adjustments restricted in range or to a particular period of brain development?

These questions can be addressed by subjecting animals to binocular prisms that shift the visual field to one side. Such prisms alter the relationship between the projection of an object's image onto the retinae and the movement required to approach the object. Adult primates, particularly humans, exhibit extremely rapid and large-scale adaptations to displacing prisms; substantial adaptations can occur within minutes or hours under optimal conditions (Held and Bossom, 1961; Harris, 1965, 1980). The mechanisms of adaptation vary with the nature of the experience. The usual mechanisms include alterations in the interpretation of (1) gaze direction (eye position relative to head, and head position relative to body), which is used to translate retinal location into a "body-centered" coordinate space, and (2) the positions of the limbs (Harris, 1963, 1980; Lackner, 1973, 1981). Although baby primates have not been tested quantitatively with displacing prisms, it seems unlikely that prism adaptation could be significantly faster or more extensive than it is in adults.

In contrast, prism adaptation in chickens is apparently much more restricted, even when prisms of moderate strength (compared to those used on primates) are placed on newly hatched chicks to maximize the likelihood of adaptation (Hess, 1956; Rossi, 1968, 1969). After days of wearing binocular displacing

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Table 1. Period of prism experience

Owl (number)	(identity ^a)	Prism strength (degree right)	Prisms on (age in days)	Prisms off (age in days)
1	Bf	11	10	65
2	Mb	11	12	75
3	OI	23	10	95
4	It	23	10	95
5	Mj	34	12	87
6	Fj	34	12	90
7	Wa	34	12	111
8	Fu	23	148	227
9	Si	23	235	275

^a Other data from some of these owls appear in other papers. The number of the owl is adapted for each report so that the order represents a logical progression for that study. The identity of the owl is maintained across studies to enable comparison of data from the same animal presented in different reports.

prisms, chicks continue to peck to one side of a target. The only evidence that adaptation has taken place is that pecking errors are made to the opposite side of the target immediately after prism removal. Although these data suggest a tremendous disparity in the adaptation capacities of chickens and primates, the task required of the chicks was different from that required of primates. Pecking is a ballistic movement made on the basis of an initial judgment of target location relative to head position. The chick loses sight of the target during the strike, and information about the accuracy of the movement is not available until after the movement is finished. On the other hand, the accuracy of orientation, approach, or pointing movements, typically used to assess prism adaptation in primates, can be evaluated and calibrated by the animal as the movements are being made. If this difference in the nature of the movements is important, it might overestimate a discrepancy in the capacities for adaptation in these different classes of animals.

The experiments reported here assess the capacity for visuomotor adaptation in another species of bird, the barn owl. The behavior used to evaluate adaptation was the accuracy with which an owl struck at a target with its talons. This behavior was chosen because it is the closest within the owl's repertoire to pointing behavior by primates. In contrast to pecking behavior, the approach of the talons during a strike is monitored visually up to the moment of impact (Fig. 1). Moreover, this behavior is included in the owl's daily experience. Nevertheless, owls that viewed the world through prisms from the day the eyelids opened exhibited little adaptation of this behavior, even though the same individuals exhibited major alterations in sound localization behavior (Knudsen and Knudsen, 1989). The visuomotor adaptation that did take place occurred in adults and in babies and resulted from modifications in motor commands rather than from changes in the perception of gaze direction or of limb positions, as in primates. The data support the contention that visuomotor plasticity is considerably more restricted in birds than it is in primates (Taub, 1968).

Materials and Methods

Subjects. Eleven barn owls (*Tyto alba*) served as subjects, 9 were used to study the effect of long-term experience with binocular displacing prisms on strike accuracy, and 2 were used only to measure normal strike accuracy (Tables 1, 2). Owls 1–7 had prisms mounted over the

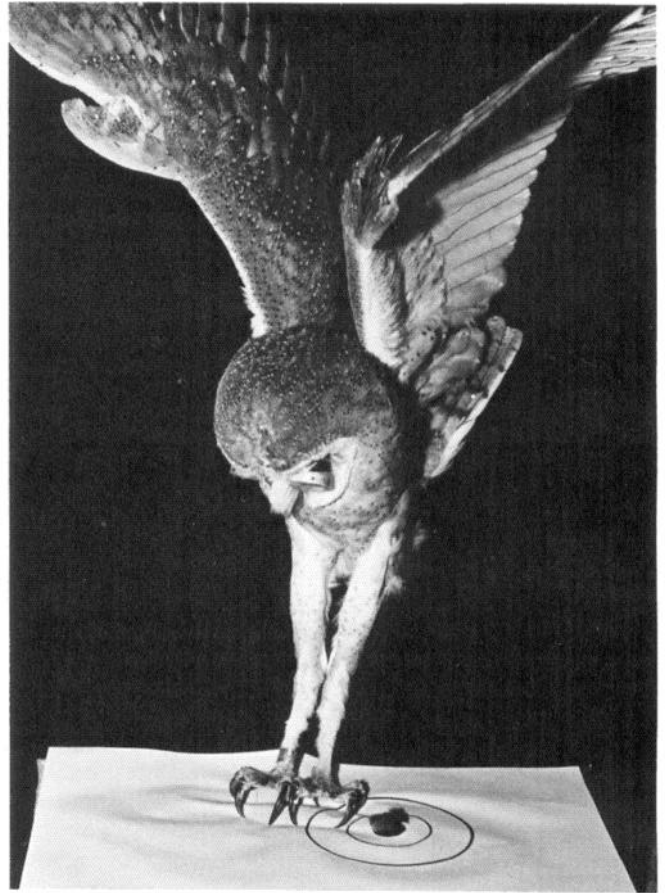


Figure 1. A strike by owl 3 after 60 d of prism experience. The owl had worn prisms from the day the eyelids first opened. The prisms displaced the visual field 23° to the right. Visuomotor adaptation is far from complete. The bull's-eye target was used for photography only. Normally, the target was placed on a uniformly white piece of paper.

eyes as babies, just as the eyelids began to open and while the ocular medium was still cloudy (Knudsen, 1989). Owl 8 was fully grown when the prisms were mounted and reached sexual maturity while wearing the prisms. Owl 9 was a sexually mature adult when the prisms were mounted. Owls 10 and 11 were juveniles between the ages of 80 and 110 d when tested.

Prisms. Owls 1–9 wore matched binocular Fresnel prisms (Vision Care/3M) of one of 3 strengths (Table 1): 20 diopter (11° displacement), 40 diopter (23° displacement), or 60 diopter (34° displacement). The prisms were oriented to displace the visual field to the right and were mutually aligned such that a collimated beam passing through either lens diffracted identically. The field of view afforded by each of the prism spectacles was measured ophthalmoscopically; detailed descriptions are given in the companion paper (Knudsen and Knudsen, 1989). In brief, the visual field decreased with increasing prism strength. However, even in the worst case (34° prisms), the horizontal extent of the visual field was 60° for the right eye and 80° for the left eye, with 50° (normal) binocular overlap. Blinders on the sides of the frames blocked peripheral vision.

The prisms were held in lightweight aluminum frames that were secured to the head with bolts. The bolts were cemented to the skull while the animal was anesthetized with halothane and nitrous oxide. Because the skull of baby owls is soft, the prisms on owls 1–7 were held in place initially by stitching the frames to an elastic helmet that was secured with chin straps to the head. When these owls reached 30 d of age, the frames were bolted to the skull as described above.

Experience. The baby owls (1–7) were raised in a single large cage where they interacted vigorously with each other and with objects in the cage. The prisms were cleaned at least once per day, and each bird was handled frequently. When the owls began to fly (about 50 d old),

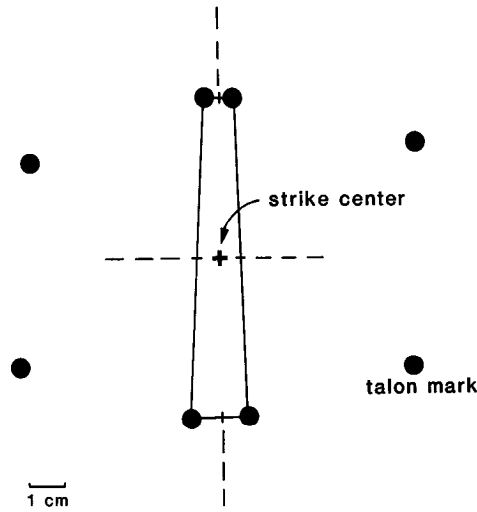


Figure 2. The pattern of talon marks that resulted from a strike. Strike center was the geometric center of the medial 2 talon marks from both feet.

training for the strike test began. At this time, the owls were placed in individual cages so that food intake could be controlled precisely. The owls continued to be handled daily as they were trained and tested.

The adult owls (8 and 9) were housed in separate cages throughout the experiment. They were much less active than the baby owls. Therefore, to encourage adaptation, we released the birds for approximately 3 hr each day in a large room where they flew among obstacles and from one perch to another.

Additional experience with those behaviors required by the experimental paradigm was gained by each bird as it was trained and tested. Nevertheless, throughout the period of prism exposure, all of the owls exhibited difficulty with landing accurately on small perches, flying through small passages, and striking at dead mice with the beak. It was apparent from these qualitative observations that the birds had not adapted completely to the prisms.

Strike test. Owls were trained to strike at a 1 cm³ piece of mouse (target) from a perch 70 cm above the floor and 60 cm from the base of the perch to the target (Fig. 1). The target was placed on a sheet of butcher paper (45 × 45 cm). Under the butcher paper was a thin pad of foam rubber. When the owl struck at the target, the talons penetrated the paper, leaving a pattern of holes (Fig. 2). A new piece of butcher paper was used for each trial. The position of the butcher paper and of the target on the butcher paper were varied from one trial to the next, although the distance of the target from the base of the perch was maintained at 60 cm.

Training the owls to perform this paradigm took about 2 weeks. Throughout the training period, the owls received food only in the test room. During the first few days of training, the birds stood on the perch and became familiar with the environment. Owls wearing prisms had more difficulty with the paradigm and, therefore, were trained on a low perch (30 cm from the ground) to begin with. When the owls became sufficiently hungry, usually by the fifth day, they would jump from the perch for food placed on the ground. Typically, they would land nearby and walk to the food. Once accustomed to this manner of feeding, they were not permitted to eat the food unless the initial approach was an

Table 2. Strike accuracy of normal owls

Owl	Sample size	Magnitude of error (mm, mean ± SD)	Azimuthal accuracy (mm, mean ± SD)
9	19	13 ± 9	Left 4 ± 11
10	27	15 ± 9	Left 6 ± 9
11	26	12 ± 7	Left 2 ± 10

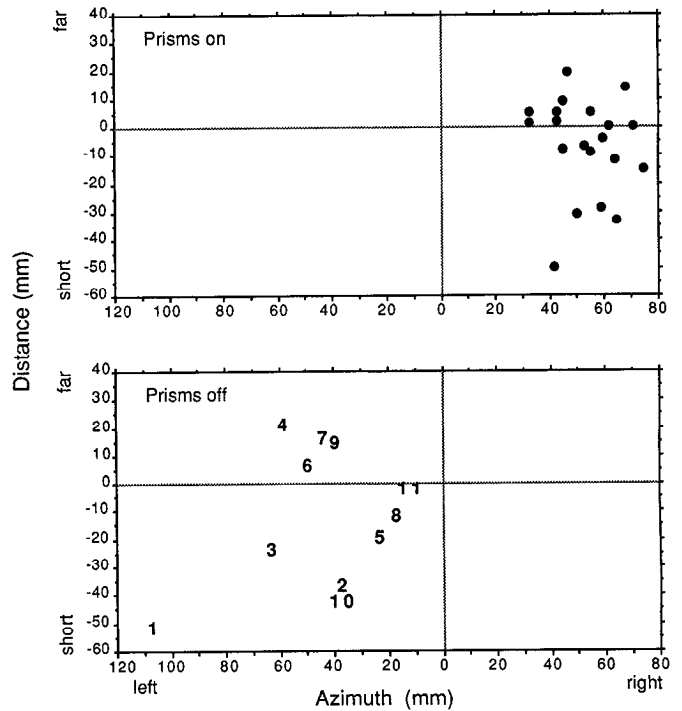


Figure 3. Strike centers of owl 4 recorded before and after prism removal. Strike centers are shown in raw form. The location of the target defined the origin of the coordinate space. Strikes with prisms on (top) were measured after 82 d of continuous experience with 23° right-displacing prisms. Strikes with prisms off (bottom) occurred in the order indicated by the numbers, immediately following prism removal.

aggressive strike. When the owls wearing prisms attained this level of training, they were placed on the 70 cm test perch to complete the training. These owls rarely hit the target with the talons, but as they landed the head moved quickly to the food.

Data analysis. After each strike, the owl's direction of approach was marked on the butcher paper. Owls either wearing prisms or with the prisms recently removed sometimes turned in the air as they descended. For these strikes, the direction of movement just before impact was recorded as direction of approach.

Strike center was quantified as the geometric center of the medial 2 talon marks from each foot (Fig. 2). Strike error was the distance from

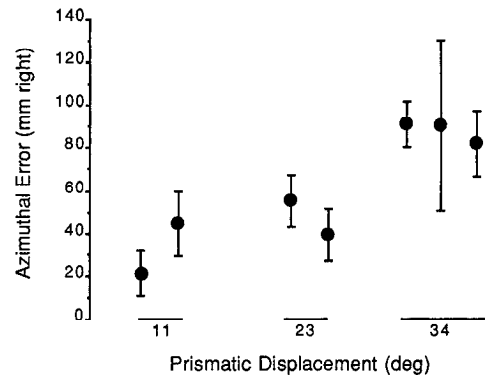


Figure 4. Mean strike error measured just before prism removal for the 7 owls raised with prisms. The azimuthal component of the strike error was defined as the shortest distance from the strike center to a line oriented in the direction of the owl's approach and passing through the center of the target. Mean azimuthal error is represented by a closed circle. The SD of azimuthal errors is represented by the bars. Sample sizes ranged from 20 to 37 strikes.

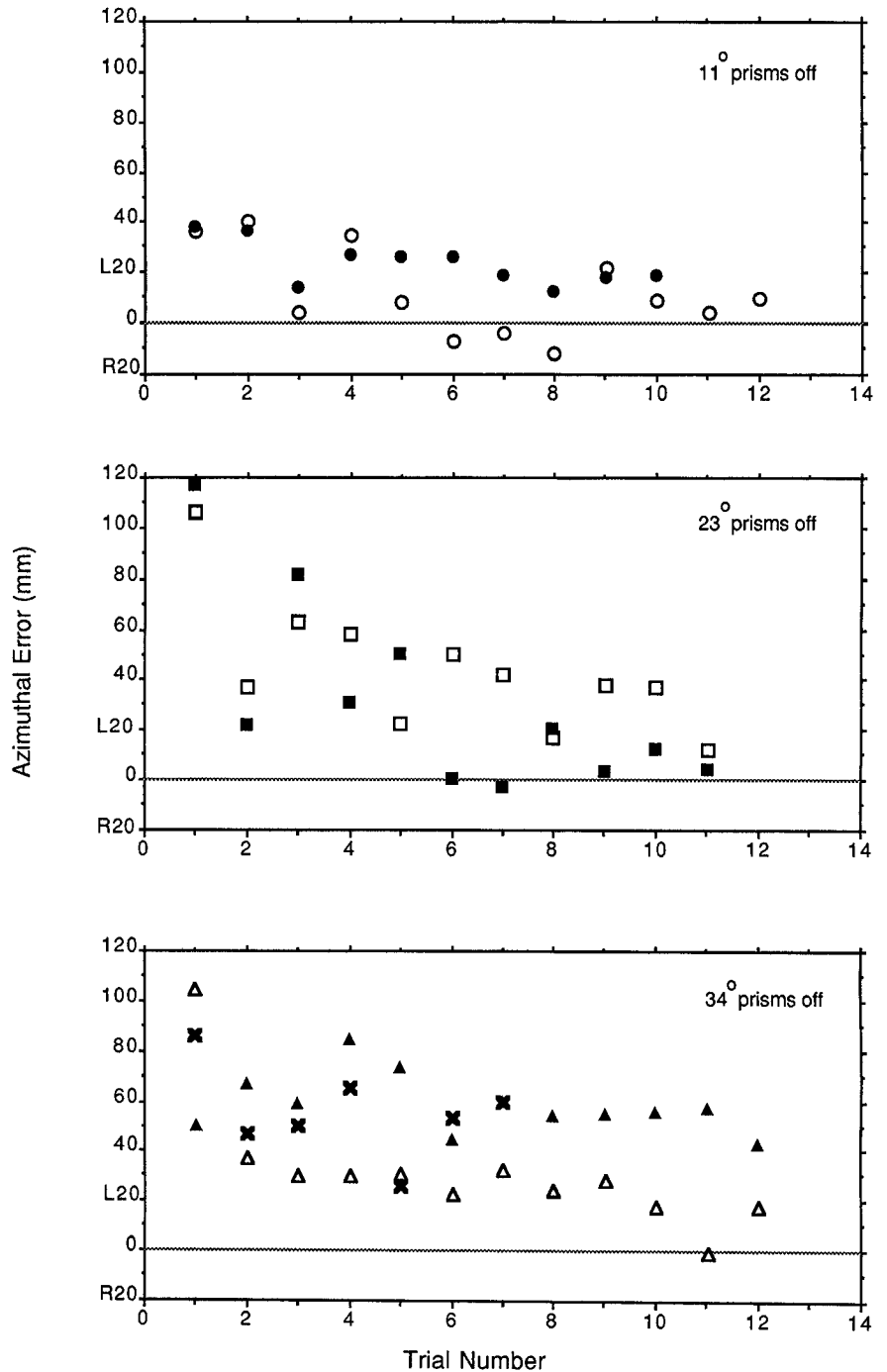


Figure 5. Recovery of strike accuracy immediately after prism removal for owls raised wearing prisms (1–7). Each symbol type represents data from one bird. Each symbol indicates the azimuthal error of a single strike plotted according to the order in which it occurred (trial number). The test sessions lasted about 30 min. The data are grouped according to the strength of the prisms worn by the owl as indicated.

the strike center to the center of the target. Azimuth error was the shortest distance from the strike center to the line passing through the center of the target along the owl's direction of approach.

Strikes by several owls were photographed with a 35 mm Nikon camera. Strikes by owls 7 and 9 during and after prism adaptation were videorecorded (Magnavox, newvicon) and were analyzed frame-by-frame (30 msec per frame) to determine speed of descent and details of adapted behavior.

Results

Normal strike behavior

Strikes carried out by 3 normal owls (owls 9–11) were stereotyped, rapid, accurate movements (Table 2). Before an owl sighted the target, it surveyed its surroundings using characteristic,

bobbing movements of the head: forward and back, up and down, and side to side. When the target was sighted, head movements ceased with the head directed at the target, and the body turned to align with the head. The head lowered slowly in the direction of the target until it was at the level of the talons. At this point, owls often paused momentarily. Then, the wings raised and the owl pushed forward, propelling the face at the target. The descent took approximately 500 msec, during which time the wings and tail made small amplitude braking movements. Just before impact, the talons swung forward in front of the face and extended toward the target (Fig. 1).

The spread of the talons always encompassed the target and was typically centered on the target. In 60 strikes by the 3 birds,

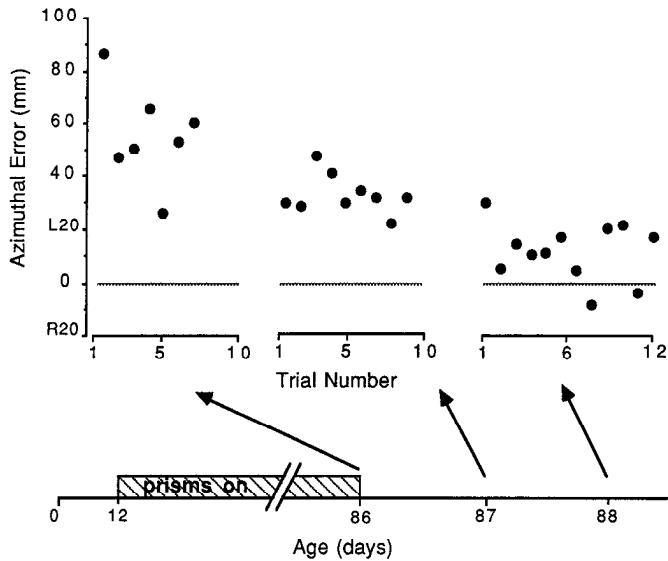


Figure 6. Recovery of strike accuracy by owl 5 following prism removal after 74 d of experience with 34° right-displacing prisms. Strike errors recorded on 3 consecutive days following prism removal (at age 86) are plotted in the order they occurred. The age line at the bottom represents the history of the bird. Hatched bar indicates the period of prism experience.

the average distance from the center of the talon spread to the center of the target was 13 mm (Table 2); the largest single error was 32 mm. For comparison, dimensions of the median talon spreads of each of these 3 owls were 80 × 97 mm, 78 × 89 mm and 66 × 113 mm, respectively.

Strike accuracy in azimuth was quantified for each owl as the transverse distance from the center of the distribution of all strikes to the location of the target (see Materials and Methods). Strike accuracy in azimuth for owls 9–11 ranged from left 2 mm to left 11 mm (Table 2).

Strike accuracy of prism-reared owls

Binocular prisms were placed on 7 baby owls at an age when the eyelids were just beginning to open (Table 1). The owls grew to full size and learned to fly while wearing the prisms. Strike accuracy was tested when the owls were between 65 and 111 d old, after having worn prisms for from 55 to 99 d. The alignment of the eyes in the head of each bird was measured ophthalmoscopically and was found to be normal. (Details of the methods of measurement and of the results have been reported previously; Knudsen, 1989.)

All of the prism-reared owls struck consistently and substantially to the right of the target (Fig. 3). Even the 2 birds wearing relatively weak prisms (11°) struck to the right by an average of 29 and 43 mm, respectively. The magnitude of mean errors increased with the dioptric strength of the prisms (Fig. 4). The data demonstrate that adaptation to the prisms was far from complete even though these animals had always viewed an optically shifted world.

Evidence that some degree of adaptation had taken place was found in the strikes carried out immediately after the prisms were removed (Fig. 3). On the first trial, carried out within minutes of prism removal, all of the birds struck to the left of the target by from 36 to 117 mm. However, the magnitude of this aftereffect decreased quickly for most of the owls (Fig. 5).

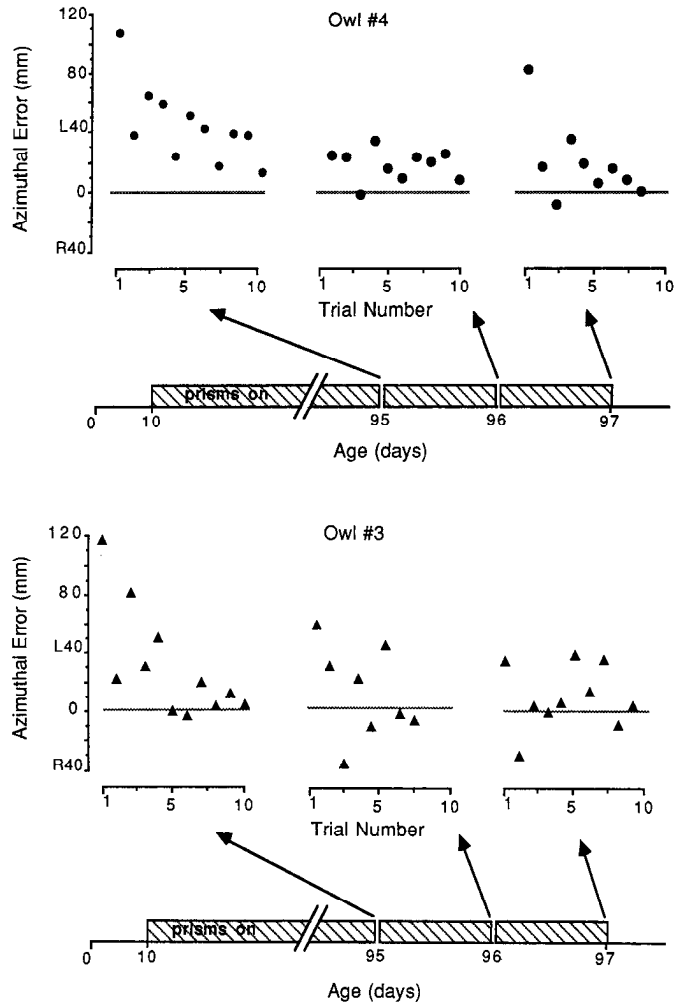


Figure 7. Strike errors of prism-adapted owls measured with the prisms removed, after which the prisms were replaced for 23.5 hr of additional prism experience. This sequence was repeated once. Strike errors are plotted in the order they occurred (trial number) for owls 4 (top) and 3 (bottom). The age line below each plot represents the history of the bird. Hatched bar indicates the periods of prism experience. Prism experience lasting 23.5 hr did not restore adapted behavior lost during the 30-min test sessions (compare with Fig. 6).

Except for 2 birds that wore 34° prisms (owls 5 and 6), all of the owls had reduced their errors by 50% after 7 trials and were striking with approximately normal accuracy (errors of less than 20 mm) by the end of the test session, which lasted about 30 min. The aftereffects exhibited by owls 5 and 6, which continued to be large throughout the first test session, were tested on subsequent days (Fig. 6); by the third day after prism removal, both owls had recovered normal accuracy.

We assume that the owls that were raised wearing prisms had already adapted as much as they would adapt by the time they were tested. Obviously, initial adaptation to the prisms by the baby owls could not be measured. However, we did test for reacquisition of the aftereffect by replacing the prisms on 2 owls (3 and 4) after they had been tested with the prisms removed. As stated previously, each of these birds struck with small errors by the end of the first test session with the prisms removed. After the test session, the prisms were replaced. On subsequent days, the prisms were again removed for testing and then were replaced. The data shown in Figure 7 indicate that the aftereffect

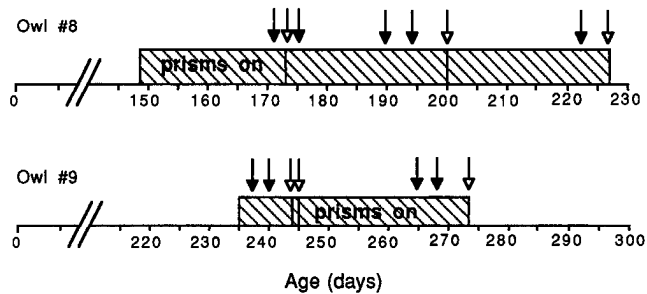


Figure 8. Histories and test schedules for owls 8 and 9. Hatched bar represents the period of prism experience. Closed arrows indicate measurements made with prisms on. Open arrows indicate measurements made with prisms removed.

observed during the first 30-min test sessions was not observed after an additional 23.5 hr of prism experience. Instead, strike errors on each subsequent day became progressively smaller. Thus, induction of an aftereffect was slow compared to the rate of loss of the aftereffect.

Prism adaptation by adult owls

Strike accuracy of 2 fully grown owls (8 and 9) was tested after adaptation periods of up to 79 d. Both birds were fitted with binocular, 23° right-displacing prisms and were tested according to the schedules shown in Figure 8. For 3 hr on each day, the owls were released in a large room containing numerous perches and obstacles and were encouraged to fly from perch to perch. The intent was to increase the owls' interactions with the environment, heighten attention, and optimize visuomotor adaptation.

Owl 9 was tested after 2 d of experience with the prisms. Strikes were extremely variable and far to the right of the target. After 4 d (Fig. 9), the consistency of strikes had improved by 50%, and the magnitude of the mean error had decreased by 20%. This slow rate of adaptation is consistent with the slow rate of reacquisition of adapted behavior observed in the young birds.

After 9 and 10 d of prism experience, strike accuracy was measured with the prisms removed (schedule: 3 hr of experience in the flight room, prisms removed for 30 min during testing, prisms replaced). On the first trial of each day, the owl struck to the left of the target by 35 and 49 mm, respectively. However, after only the second or third trial, the error was less than 20 mm. Experience with the prisms resumed for an additional 20 d (for a total of 30 d), after which strike accuracy was reassessed. Although still striking well to the right of the target, the owl had improved accuracy and precision compared to when it was last tested with the prisms in place (on day 4). After a total of 38 d of prism experience (except for the two 30-min test sessions on days 9 and 10), the prisms were removed permanently, and strike errors were measured. As was observed on days 9 and 10, strike error was large on the first trial but declined rapidly and was within a normal range by the end of the test session (Figs. 9, 10).

Owl 8 was tested periodically for strike accuracy during 79 d of prism experience (Fig. 8). The results were similar to those reported above for owl 9. With prisms on, the bird struck far to the right of the target even after 75 d of prism experience. Following prism removal, the initial strike was far to the left,

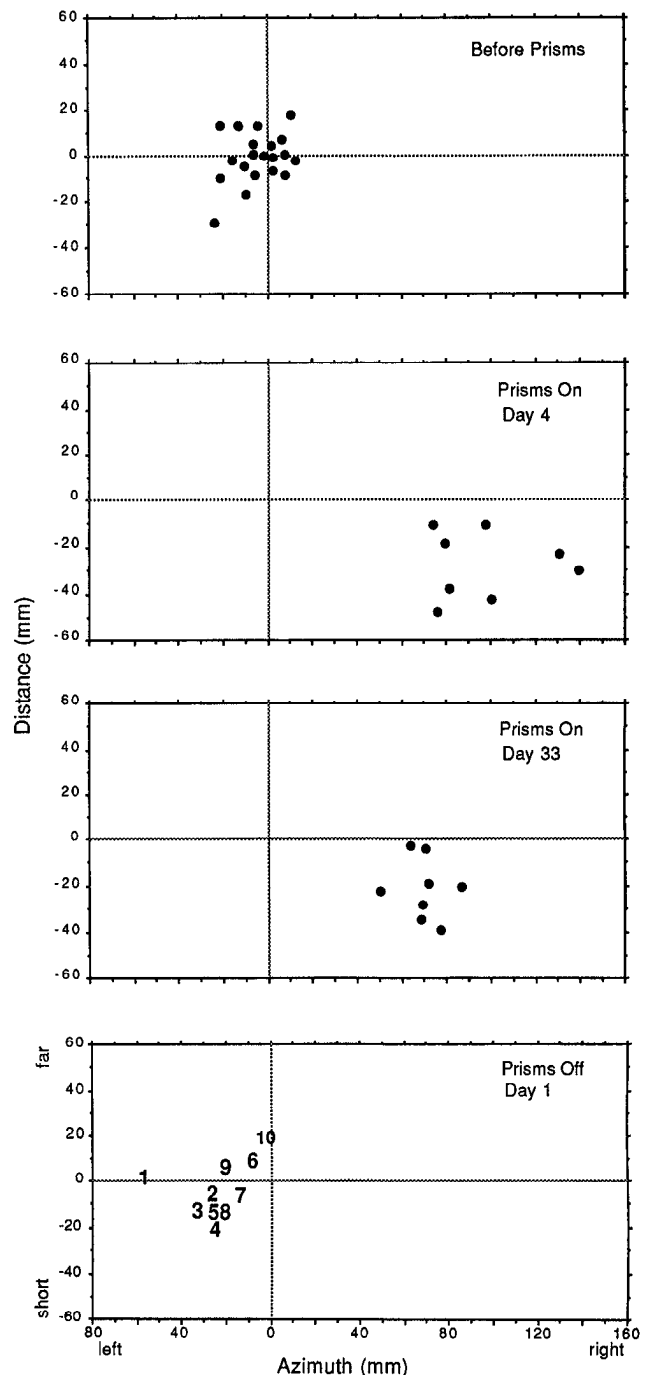


Figure 9. Distribution of strike centers recorded from an adult owl (9) before, during, and after experience with 23° right-displacing prisms. The location of the target defined the origin of the coordinate system for each plot. The numbers in the bottom plot (prisms off) indicate the order in which the strikes occurred. The systematic distance error with the prisms on suggests a small vertical component to the optical displacement induced by the prisms.

but strike error diminished rapidly on subsequent trials and was normal by the fourth strike (Fig. 10).

Alterations in attack behavior resulting from prism experience

The attack behavior of owls wearing prisms was altered by prism experience. When the owls viewed the target through the prisms, the head was oriented to the right of the target (as expected from

the optical displacement caused by the prisms). The magnitude of the misalignment of the head relative to the target increased with the strength of the prisms worn by the owl. The body turned to align approximately with the misdirected head. Instead of moving the head straight forward from the body, the head moved diagonally leftward until it was over the left talon. The birds wearing 11° prisms and 2 of the birds wearing 23° prisms pushed off to the left on a diagonal trajectory toward the target. The other owls often made leftward turns of from 45° to 180° as they descended. The wings flapped asymmetrically as the owls attempted to correct the trajectory of their approach. Before impact, the talons extended either in the direction of or to the left of the path of descent (toward the target).

As soon as the prisms were removed, the owls attended to targets with the head oriented directly at the target. As the head lowered, it moved to the left (as it did with the prisms on) until it was over the left talon (Fig. 11, trial 1). When the owl pushed off, the body also moved off to the left. Asymmetrical movements of the wings and, occasionally, a rightward turn (of up to 90°) reduced what would have been a larger error. In addition, the talons often extended to the right of the path of descent (toward the target).

Videorecordings made of owl 7 before and after prism removal revealed additional details of the adapted behavior. The initial leftward translational movement of the head and the leftward thrust of the body as the owl pushed off were the two most salient behavioral adaptations. After the prisms were removed, these movements caused the head to become misaligned with respect to the target as the owl descended (Fig. 11, trial 1). Frame-by-frame analysis showed that the head realigned with the target with a saccadic movement that caused the head to be turned relative to the body and relative to the direction of travel. The asymmetrical movements of the wings tended to restore alignment of the body with the head and altered slightly the direction of travel.

After the tenth strike with the prisms removed (20 min after prism removal), the misdirected leftward movements of the head and body did not occur, and the strikes appeared identical to those carried out by normal owls (Fig. 11, trial 11).

Discussion

Owls adapt visuomotor behavior in response to binocular displacing prisms, both as adults and as babies. With prisms on, improvement of strike accuracy takes place over a period of weeks (at least in adults; Fig. 9). The improvement in accuracy results from the modification of movements used to approach objects. The owls learn to move the head and body laterally relative to the orientation of the head (Fig. 11, trial 1). Despite these adapted movements and the use of trajectory correction during approach, owls continue to make large strike errors even after months of continuous prism experience. In contrast, adult primates can adapt pointing behavior and spatial perception almost completely within hours in response to comparable (10° to 20°) prismatic displacements (Hamilton and Bossom, 1964; Harris, 1965; Taub, 1968; Lackner, 1973). Clearly, the capacity for visuomotor adaptation by owls is extremely limited by comparison.

When prisms are removed from prism-adapted owls, the owls strike to the opposite side of the target. The absolute magnitude of adaptation cannot be determined from the strike data because the test paradigm permitted error correction during the approach. However, the rate of adjustment following prism re-

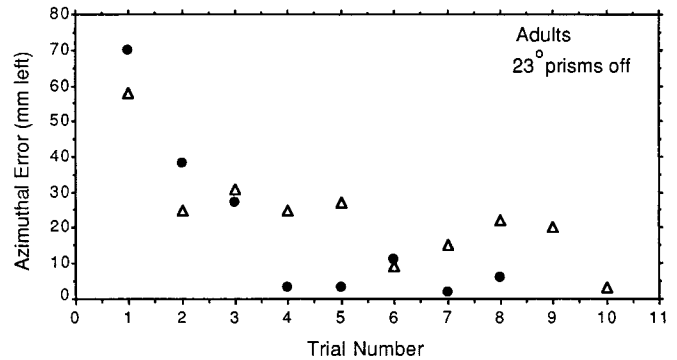


Figure 10. Strikes by adult owls immediately after prism removal. Closed circles are data from owl 8. Open triangles are data from owl 9. The strike errors are plotted in the order they occurred. The test sessions lasted about 30 min. The owls wore 23° right-displacing prisms for the periods indicated in Figure 8.

moval, as indicated by the strike tests (Figs. 5 and 10) and as corroborated by the loss of adapted behaviors observed on videorecordings (Fig. 11), demonstrates a very rapid adaptation process following prism removal.

Mechanisms of prism adaptation

To approach an object, an animal must interpret accurately or calibrate the following: (1) image position on the retina, (2) eye position relative to the head, (3) head position relative to the body, (4) limb positions relative to the body, and (5) motor commands to move the limbs. Alterations of the first 3 would change the perceived locations of objects. Alterations of the last 2 would change the way the body moves toward a perceived object.

Humans and cats that are strabismic at an early age sometimes reinterpret image position on the retina of the deviated eye(s) and develop what is referred to as "anomalous retinal correspondence" (Duke-Elder and Wybar, 1973; Olson, 1980). These individuals fixate on an object with the eye oriented to one side, yet localize the target accurately. The owls did not do this. The positions of the eyes of prism-adapted birds were aligned normally in the head (Knudsen, 1989), and immediately after prism removal, the head aligned accurately with the target.

The mechanism used by humans to adapt to displacing prisms depends on the nature of the experience. One important mechanism is the alteration of the perceived direction of gaze (Harris, 1965; Lackner, 1973). Individuals who have adapted appropriately to prisms interpret the head as being straight on the body when actually the head is turned to the side in the direction that compensates for the optical displacement caused by the prisms. When the head is held in alignment with the body, it is perceived as turned to the opposite side. If the person is asked to look straight ahead with the head in this position, the eyes deviate in the head in the direction that compensates for the prisms (Lackner, 1973). As a result, the position of a target that is perceived as being straight ahead with the prisms on is, in fact, directly in front of the body.

Prism-reared owls do not alter the rest positions of the eyes (Knudsen, 1989), and it is therefore unlikely that they change their interpretation of eye position in the head. However, owls do make extensive head movements, large in amplitude (up to $\pm 80^\circ$ in the horizontal plane) and in every plane of space (roll, pitch, and yaw). If the owl is to maintain perceptual stability

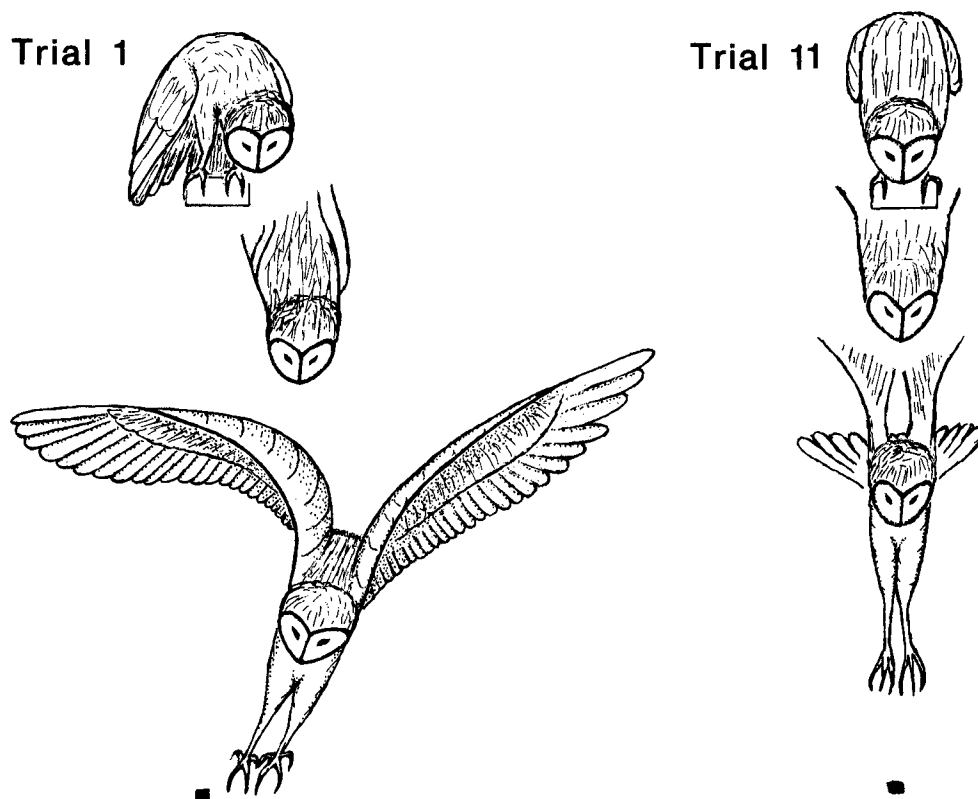


Figure 11. Strikes by a prism-adapted owl immediately after prism removal. Tracings of owl 7 were made from videorecordings of strike 1 and strike 11 (open triangles in Fig. 5) carried out immediately after 34° right-displacing prisms were removed. Sequential tracings are at 300-msec intervals. In both strike sequences, the head and body initially aligned with the target. The first image from trial 1 shows the owl after it moved the head to the left at the beginning of the attack. In the frame following the second image, the head made a saccadic turn to the right.

during head movements, it must account for head position when computing stimulus location. Thus, an obvious mechanism for the owl to use to adapt to prisms is to alter the perception of head position relative to the body. With the prisms on, the owls could have localized objects accurately simply by perceiving the head as being straight on the body when, in fact, it was turned to the right (as humans would do). This is not what the owls did. When owls wearing prisms attended to a target and prepared to attack the target, the body was aligned normally with respect to the head, and both the head and body were misaligned relative to the target. The owls neither stood nor flew with the head turned to the right of the body. Immediately after prism removal, when the owls prepared to attack a target, there was no tendency for the body to be turned to the left relative to the head (or to the target). Instead, the head and body aligned accurately with the target. The results imply that the owl's sense of head position is not altered by prism experience, unlike that of humans (Harris, 1965; Lackner, 1981).

The mechanism used by owls to adapt to displacing prisms was to alter the movements employed for approaching targets. Prism-adapted owls initiated an attack with a leftward translational movement of the head. With the prisms on, this movement was appropriate to cause the image of the target to remain at a constant position on the retinae. When the animals pushed off from the perch, they did so with a leftward thrust of the body, which also tended to stabilize the image of the target on the retinae. However, the angle of these leftward movements was not adequate to compensate for the optical shift caused by the prisms. Because the approach was still too far to the right, the retinal image of the target moved to the left as the owl approached. In response, the owls made additional leftward movements as they closed on the target.

With the prisms removed, these adapted movements were inappropriate. The leftward movements caused the owl to miss to the left of the target and caused the retinal image of the target to slip to the right. To attend to the target, the owls made saccadic head turns to the right as they descended. Visual feedback during these strikes contradicted the acquired behavior patterns, and they disappeared rapidly.

Adjustment of motor commands could underlie prism adaptation in chickens and may also be a component of prism adaptation in primates. The capacity of primates to calibrate voluntary and reflexive movements using visual feedback is extensive. However, because our sense of head, eye, and limb position is so plastic, there remains little need for motor adjustments in prism adaptation.

Rate of prism adaptation

Owls adapt to displacing prisms slowly. In adult birds, the process continues for weeks (Fig. 9). In young birds, although the time course of initial adaptation was not measured, the prism aftereffect that disappeared during a brief (30-min) exposure to normal vision did not reappear after subsequent 23.5-hr exposures to displaced vision (Fig. 7). This is opposite to the cumulative effect of repeated prism exposure on aftereffect observed in humans (Yachzel and Lackner, 1977). The slow rate of prism adaptation in owls contrasts sharply with the rapid rate exhibited by primates. These differences could be due either to phylogenetic differences in plasticity or to differences in motor adjustment (owls) versus proprioceptive adjustment (primates) or to both.

Owls extinguish prism-adapted behavior quickly following prism removal. Owls that grew up wearing prisms (1–7) had always to move the head and body to the left relative to the

orientation of the head in order to approach an object. Yet 5 of these owls learned within 30 min of prism removal to approach an object by moving the head and body straight ahead (Fig. 5).

The discrepancy in the adaptation rates to displaced vision versus to normal vision indicates a strong and apparently innate predisposition of the brain to use normal, symmetrical motor commands to approach objects. Adapted, asymmetrical motor commands require continuous visual feedback to be maintained: 30 minutes of normal vision were usually enough to eliminate long-standing adapted behavior (Fig. 7). A similar but far less extreme discrepancy in adaptation of pointing movements occurs in humans as well (Hamilton and Bossom, 1964).

Magnitude of prism adaptation

The range of prism adaptation is small in owls, as in chickens (Hess, 1956; Rossi, 1969). Even owls that view a displaced visual field throughout their lives as they learn to fly and to interact socially continue to make large visuomotor errors. Clearly, the neural circuitry that underlies visual localization and approach movements is extremely resistant to modification by visual experience. The apparent lack of proprioceptive plasticity, such as that exhibited by primates, cannot be explained by a general lack of mechanisms for visually guided adjustment of sensation in owls. Auditory localization, for example, is modified substantially by prism experience and by chronic monaural occlusion (Knudsen et al., 1984; Knudsen and Knudsen, 1989). Both manipulations cause the auditory system to reinterpret localization cues according to spatial information provided directly or indirectly by the visual system (Knudsen and Knudsen, 1985). Thus, in birds as in mammals, vision is the ultimate source of information for calibrating space perception as well as movements. A major difference seems to be that, in primates, vision calibrates proprioception, whereas in owls, the sense of head and limb position is established by mechanisms that appear to be largely independent of vision.

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