DEVELOPMENT OF VISUAL ACUITY IN TWO SPECIES OF PEROMYSCUS (RODENTIA)

Thesis for the Degree of Ph.D.

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BEDFORD MATHER VESTAL

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ABSTRACT

DEVELOPMENT OF VISUAL ACUITY IN TWO SPECIES OF PEROMYSCUS (RODENTIA)

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Peromyscus maniculatus bairdi, a terrestrial grassland rodent, and P. leucopus noveboracensis, a semi-arboreal form, were used as experimental subjects to: 1) describe visual acuity and ontogeny of vision in a nocturnal rodent; 2) determine whether evolutionary adaptation to different habitats has led to differences in visual development; and 3) determine the effect of stimulus distance and ambient illuminance on visual acuity. Visual acuity, the resolving power of the visual system, is the resultant of several environmental and morphological factors and was used as an indicator of visual maturation.

The mice were restrained on a platform within a rotating drum which could be lined with equal black and white stripes of various widths. The minimum separable visual angle was the measure of acuity. If the stripes were large enough to be seen, an optokinetic nystagmus response was exhibited by the mice. A maximum of eight trials of 15 seconds duration were given for each stripe width. The angle subtended by the smallest stripe eliciting a response

in each direction of drum rotation was the visual angle for that subject. Stripes differed by 7' (minutes of arc) increments. A cross-sectional design was used, with age after eye opening, stimulus distance (10 cm, 20 cm, and 40 cm), and light intensities (4.3 lux, 86.1 lux, and 861.1 lux) as the main variables. Two-hundred forty-eight mice were tested. The smallest stimulus stripe sizes available at each distance (35' at 10 cm, 21' at 20 cm, and 14' at 40 cm) limited determination of the minimum thresholds of acuity for some mice.

Both species had average acuities of 18.2' visual angle at 40 cm, 8 days after eye opening. Individuals responded to 14' stripes as early as 4 days after eye opening. These values represent the smallest visual angle reported for any rodent. At 20 cm stimulus distance the mean visual angle of leucopus dropped significantly one day before that of maniculatus. At 40 cm maniculatus' mean decreased one day before leucopus'. The developmental patterns of the two species were otherwise similar. Acuity improved significantly with age. The pattern of results during development was significantly affected by stimulus distance. The limits of stripe size were seen by all mice on the day of eye opening at 10 cm (35'), by 95% of the mice at two days after eye opening at 20 cm (21'), and by 85% of the mice at six days after eye opening at 40 cm (14'). Threshold visual angles at comparable ages were significantly smaller at

20 cm than at 40 cm. The illuminance levels used had no significant effect on visual acuity. Size of visual angle was significantly and negatively correlated with body weight and age at the time of testing.

There was no consistent relationship between species' habitat and developmental pattern. The visual system matured rapidly, and vision was more acute than in other rodents which have been studied.

DEVELOPMENT OF VISUAL ACUITY IN TWO SPECIES OF *PEROMYSCUS* (RODENTIA)

By

Bedford Mather Vestal

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INTRODUCTION

The age of an animal when it encounters various types of stimuli can contribute to its adult behavior. Early experience variables are related to the developmental state of an animal's sensory systems at the time it receives the stimuli. The resolving power of a sensory system can affect the quality and quantity of stimulus input and thus determine the quality of early experience which may shape adult behavior. Species differences in behavior may be partly due to differential patterns of sensory development (King, 1961a).

Many adult behavior patterns are visually mediated, and since early visual experience affects later behavior, it is necessary to know the developmental pattern of visual acuity (the resolving power of the visual system) in relation to the development of behavior.

The morphology of the visual system, which varies between species and with developmental state, can affect visual acuity (Rahmann, 1967). The distance of the stimulus from the eye also affects acuity because of limitations on accommodation and depth of focus imposed by eye structure (Walls, 1967). Since vision is based on light, acuity may be limited by the ambient illuminance (Riggs, 1965) and the light gathering power of the eye (Walls, 1967). A comparative developmental study of visual acuity, which includes the

manipulation of stimulus distance and ambient illuminance, was needed to determine the relationship of these factors to each other.

Comprehensive studies of this type have not been reported. Most comparative studies utilize only adult subjects and are made across broad phyletic lines (Rahmann, 1967). Comparisons of relatively closely related species are needed in studying the evolutionary effects of various ecological factors on vision and its development. The single comparative developmental study to date (Ordy, Latanick, Samorajski, and Massopust, 1964) only used small numbers of animals from several primate genera. Their study had the additional disadvantages of a longitudinal type of design (which may confuse testing experience with development) and lack of any indication of variability in the responses. Weymouth (1963) points out the need for indications of variability in visual acuity and statistical analysis of the data for evaluating the vision of a group or species. While most animals lack visual accommodative mechanisms (Walls, 1967), no work on the developmemt of visual range in this type of animal has been reported. The effects of illuminance levels on visual acuity in human beings and other diurnal animals have been well shown (Rahmann, 1967), but only two studies have been done on nocturnal animals (Rahmann, Rahmann, and King, 1968; Neuweiler, 1962).

The primary aim of this study was to describe the visual acuity and development of acuity in two relatively closely related species of nocturnal rodents and to experimentally determine the effect of stimulus distance and illuminance on visual acuity in the developing animals. By using a cross-sectional design, measuring acuity with relative precision, and indicating the variability of response, this experiment was meant to provide a more accurate analysis of development of visual acuity than was previously available.

LITERATURE REVIEW

Definition and Methods of Measurement

Visual acuity is the capacity to resolve details of objects in the visual field, specified in terms of some critical measurement of the stimulus objects. Acuity is the reciprocal of the angle (in minutes of arc) subtended at the eye by this critical measurement (Riggs, 1965).

Four major types of visual tasks are used to measure visual acuity. For humans these are described as: 1. detection - detection of a test object in the visual field; 2. recognition - name test object or name or specify some critical aspect of it; 3. localization (or vernier acuity) - discrimination of small displacements of one part of the test object with respect to other parts; 4. resolution (or simple discrimination) - response to a separation between elements of a pattern (Riggs, 1965). The resolution task has been used most often to test visual acuity of non-human animals because it can generally be determined more easily by objective behavioral responses.

Tasks 1, 2, and 3 provide a measurement of the minimum visible, the smallest single object or feature which can be seen. Resolution provides the minimum separable, the minimal distance between two visual objects (i.e. two points

or lines) which can be discriminated as separate. In both cases the angle subtended at the eye by the critical measurement is defined as the minimum visual angle (or visual angle) in degrees, minutes or seconds of arc. It is a measure of the maximal resolving power of the eye being tested (Rahmann, 1967). In most cases minimum visible angles are smaller, indicating better acuity for these types of tasks, than minimum separable angles.

Four objective behavioral measures of visual acuity have been described: 1. Visual cliff (Walk, 1965); 2. Visual preference or fixation (Fantz, Ordy, and Udelf, 1962); 3. Simultaneous discrimination (Lashley, 1930; Rahmann, 1966); 4. Optokinetic response (Warkentin and Smith, 1937; Reinecke and Cogan, 1958; Suthers, 1966). The visual cliff and discrimination methods require ambulatory abilities which are often poorly developed in young animals. Discrimination also can confound sensory development with discrimination learning. Visual fixation requires close restraint of the animal, a method of determining pupil position, and relatively high arousal or attention levels, all of which make the method difficult to use in many species.

The optokinetic response is a reflex visual response to a moving visual field. The nystagmus consists of two phases: 1. a slow or pursuit phase in the direction of

stimulus movement; 2. a fast or return phase opposite in direction to stimulus movement. The eyes, head and body may exhibit the response (Smith and Bojar, 1938).

The optokinetic response was chosen for this study because it involves a discrete motor response which is well developed at the age when vision becomes functional (Ordy, Massopust and Wolin, 1962; Vestal and King, 1968). It has been used in other developmental studies of visual acuity (Warkentin and Smith, 1937; Ordy et al, 1962; Ordy et al, 1964). Results from human beings indicate a high correlation between acuity values found by the optokinetic method and values from standard Snellen tests. However, the optokinetic visual angles were consistently larger than results from Snellen tests (Reinecke and Cogan, 1958). Wolin and Dillman (1964) used a different optokinetic method with human adults and also found a high correlation with the Snellen method. Their results showed relatively smaller optokinetic visual angles for subjects with poorer acuity. Fantz et al (1962) compared visual fixation and optokinetic tests in human infants. The results corresponded closely at most ages with lower optokinetic thresholds at one to two months of age.

The principal objection to the use of this response as a test for acuity is that in animals with foveate retinas, the periphery of the retina contributes more to the response than the foveal area. Tests of peripheral vision will show

a lower value of acuity than tests involving primarily the fovea (Riesen, 1960; Riggs, 1965; Rahmann, 1967). The above comparisons suggest that this is not a valid criticism. This problem can be avoided by testing subjects without foveate retinas. Although the optokinetic response can provide the minimum visible angle (Smith and Warkentin, 1939), it is usually used, as in this study, to find the minimum separable angle (Smith and Bojar, 1938).

Factors Governing Visual Acuity

Various factors affecting visual acuity are reviewed for human beings by Riggs (1965) and Lit (1968) and on a comparative basis by Walls (1967). Three of these factors, morphological structure, stimulus distance, and light intensity, will be discussed here, primarily as they have been studied in rodents and as they apply to the present study.

Morphological structure may limit the maximal visual acuity of a species. The fineness of the retinal mosaic, both in size and density of visual receptor cells and in degree of nervous summation, may in many species be the ultimate limiting factor (Rahmann, 1967). Acuity should be best in that part of the visual field where the density of receptors is highest and/or where there is less summation of receptors on ganglion cells and optic nerve fibers. Although rats and mice do not have retinal foveas,

there is a decrease in the ratio of rod nuclei per ganglion cell (decrease in summation) from periphery to center in the rat retina (Lashley, 1932). This would indicate the possibility of higher acuity for images projected on the central part of the retina and would explain the eye movements seen in visual fixation in rats (Lashley, 1932). With a homogeneous retinal mosaic there would be no need of fixation movements. Retinal summation appears to be greater in mice (63-89 rod nuclei per ganglion cell) (Menner, 1929; Bucciante and DeLarenz, 1929, as cited in Lashley, 1932) than rats which have ratios varying from 27:1 at the approximate center to 78:1 at the periphery. Although the part of the retina from which mouse cell counts were taken was not given, Lashley (1932) indicates that on the basis of these counts visual acuity in the house mouse must be poorer than in the rat.

Quality of the visual image is further affected by the cornea, pupil opening and lens. Walls (1967) discusses the adaptation of mouse and rat eyes for nocturnal life. Their almost spherical lenses, along with the large cornea and pupil, act to maximally brighten the retinal image in dim light. Walls feels that this arrangement along with a rather homogeneous retinal mosaic obviates the need for eye movements by providing a wide field of vision, although rats and deermice exhibit distinct eye movements (Lashley, 1932; personal observation).

The morphology of the cornea and lens systems affect visual image quality by focusing the image on the retina. Shape and size of the lens, as well as its ability to accommodate, determine the range of distances at which objects will be seen most sharply (Rahmann, 1967). Mice have degenerate ciliary muscles indicating that they have probably lost the ability to accommodate. They apparently have a nearby focal point, and everything is in focus from there to the eye (Walls, 1967). Lashley (1932) found Norway rats to be very myopic, with the sharpest focus of objects at 7.5 to 8 cm from the cornea. However, he felt that in such a small dioptric system with relatively large functional units in the retina there is considerable depth of focus which permits nearly equal detail vision over a wide distance range, even without accommodation. Lashley could view objects ranging from 15 mm up to 20 meters away in some detail through the excised eye of an albino rat. Rahmann, Rahmann and King (1968) indicate optimal visual ranges (a behavioral measure of focal length) for several species of deermice ranging from 4.0 to 11.0 cm. However, their method involved increasing stimulus distance without corresponding increase in stimulus size. At greater distances the stimulus objects would be relatively smaller. Thus their measure of visual range would be strongly affected by the visual acuity of the species (Graham, McVean, and Farrer, 1968) and is probably not a good measure of actual optimal focal length. The values should be larger

than those reported. All of the above evidence indicates that nocturnal rodents such as rats and mice are rather myopic.

The range of detail vision can be tested by using stimuli subtending corresponding visual angles at different distances. Only a few species have been tested in this way. Human infants accommodate very well from 5 to 20 inches distance (Fantz et al, 1962). Primates, such as the rhesus monkey, have good accommodation and exhibit no differences in acuity at 3 feet and 20 feet (Graham et al, 1968). Two cats tested by Smith (1936) had higher acuity at 75 cm distance than at 50 or 100 cm. Walls (1967) indicates that among mammals the extent of accommodation is poor except in primates. Lashley (1932) was not able to accurately determine the change in resolving power with changes in stimulus distance in excised albino rat eyes.

Visual acuity is generally better under higher than lower light intensities. In animals with mixed rod-cone retinas, acuity plotted as a function of the logarithm of light intensity generally follows a rising sigmoid curve. The lower leg of the curve indicates rod function; the rising portion and level part represent increasing stimulation of cones. Rahmann(1967) reviews these results in vertebrates. However, in the only acuity test of a nocturnal animal with an all rod retina (flying fox bat) where light intensity was systematically varied, acuity merely leveled off at the higher light levels used (Neuweiler,

1962). Results with deermice indicated that acuity was somewhat better at the highest of 3 levels of illuminance tested (Rahmann et al, 1968). In a nocturnal animal there could be a possibility of dazzlement and consequent loss of acuity. However, the human pupil appears to adapt to optimum apertures for acuity at different light intensities (Campbell and Gregory, 1960) and since the rat has a good pupillary reflex (Lashley, 1932), this effect could probably be ruled out. The pupillary reflex in mice has not been studied. The enlarged pupil at low intensities increases optical abberations in the human eye (Riggs, 1965), but the effect of this factor in eyes which have evolved for function at low illuminance levels is not known.

Species Differences In Visual Acuity

Species differences in adult visual acuity have been reviewed by Rahmann (1967) over a wide variety of vertebrates. Polyak (1957) and Walls (1967) compared the visual systems of vertebrates and discussed structural and functional differences in visual equipment which may be the basis of acuity differences. These structural and functional differences have presumably evolved as the result of different environmental demands on the animals, and comparative studies of visual acuity can perhaps point out some of these environmental demands. A primary reason for

doing comparative studies of vision is to help point out the genetic basis for visual behavior. A major problem of comparative studies has been with the use of widely divergent phyletic groups which may obscure genetic factors (King, 1968a). In recent years a few workers have begun comparing rather similar forms and attempting to relate the results to the life history of the animals. Cowey and Ellis (1967) attempted this with rhesus and squirrel monkeys. Suthers (1966) obtained approximate visual acuity scores for 8 genera of bats but his results should be carried further using much smaller stimuli. Comparative studies of rodents have not been extensive. Rahmann (1966) compared the acuity obtained by discrimination learning in 2 genera of lemmings. The best score for mountain lemmings (Lemmus lemmus) was 36' of arc at 6 cm distance and that of wood lemmings (Myopus schisticolor) was 71' at 4 cm. Lashley (1938) used a jumping stand discrimination test to obtain visual acuity values of 24-35' for pigmented laboratory rats (Rattus norvegicus) and 1^{o} 10' - 1^{o} 20' for albinos. Rahmann et al's (1968) paper on adult deermice is the only study to date on visual acuity of several closely related species of mammals (see Table 1 for their results). The results are not strictly comparable to those of the present study because they used a discrimination learning technique. They sometimes used the same stripe width at different distances to obtain different angles for testing. This

TABLE 1 VISUAL ACUITY AND VISUAL DISTANCE IN *PEROMYSCUS*[a]

	0.1 Ft. Candle		1 Ft. Candle		10 Ft. Candle	
	VA[b]	Distance[c]	VA	Distance	VA	Distance
P. floridanus	-	-	1°	5.0	-	-
P. polionotus	1° 34'	3.8	2°	3.5	1° 47'	4
P. m. bairdi	54'	3.8	54'	6.5	54'	6.5
P. m. gracilis	1° 11'	8	33'	7	29'	8
P. californicus	1° 25'	11	38'	11	38'	11

[a] Compiled from Rahmann *et al*, 1968

[b] Smallest individual visual angle

[c] Distance in cm

procedure may confuse visual acuity with ability to accommodate (Graham et al, 1968). The four comparative studies of visual acuity in rodents all used discrimination learning techniques, and all tested only adult animals.

Development of Vision and Visual Acuity

Just as species differences in visual equipment affect visual performance so does the stage of development. The ontogeny of visual parameters such as depth perception (Walk, 1965b), visual preference (Fantz, 1965), sensorimotor coordination (Hein and Held, 1967) and morphological development (Samorajski, Keefe, and Ordy, 1965) have been studied in some species (see also Riesen, 1960 for a review). Visual acuity and the range of optimal vision should also improve during development as the eye increases in size and the neuromuscular systems mature (Rahmann, 1967).

Baerends, Bennema, and Vogelzang (1960) found a smooth decrease in the minimum resolvable visual angle during the development of the cichlid fish Aequidens. However, development may have been confused with learning in the discrimination technique used. Warkentin and Smith (1937) elicited optokinetic responses to four sizes of stimulus angles to demonstrate the gradual development of visual acuity in kittens. The kittens required an average of 11.2 days after eye opening to develop a response to the smallest angle tested, 11' of arc. Development of acuity

in rabbits seems to occur saltatorily rather than gradually as in kittens. First appearance of the optokinetic response occurred at about the same time the cornea and lens became transparent (Warkentin, 1937). Ordy et al (1962) found that in rhesus monkey infants visual acuity (optokinetic test) matured much more rapidly than did postnatal retinal differentiation as determined by fundoscopic examination. Four stimulus angles were used in the acuity test. Further studies indicated that the rhesus reached adult levels of acuity (1' of arc, discrimination technique) by 2 months of age but again only four stimulus angles were used (Ordy et al, 1965). Morphological studies of the retina showed that peripheral cones had completed ultra-structural development at birth while foveal cones were structurally mature by 2 months of age (Samorajski et al, 1965). The peripheral development apparently is correlated with maturity of the optokinetic response while foveal maturation would allow adult performance in the discrimination test. Developmental studies of acuity in 4 genera of primate infants and human infants indicated that rhesus and baboons matured faster than a gibbon and an orangutan, and they all matured faster than human infants. The data are not presented in a form which can be compared readily to other studies (Ordy et al, 1964). Some data on the development of acuity in human infants and children are also available (Slataper, 1950; Fantz et al, 1962; Weymouth, 1963). Weymouth

emphasized that good measures of variability are missing from the data available on human beings, largely because many of the data have been derived from various clinical tests. The overall review of the visual acuity development studies found that they shared common problems. They generally involved very few subjects. Few stimulus angles were used for testing, and they were of such sizes as to preclude statistical analysis of the data. In addition, information was not available for many important groups of animals such as the rodents.

Little information is available on other aspects of visual development in mice. DeRobertis (1956) has done anatomical studies of rod ultra-structural development in Mus musculus. Dapson (1968) found developmental changes in lens proteins of Mus which slowed or reversed at about seven months of age. In several strains of Mus the eyes opened at 11-13 days of age, and a visual placing response was first elicited reliably at 14 to 15 days (Fox, 1965). Lens weight in Peromyscus leucopus increased rather rapidly until about 25 days of age, but growth was not measured past 30 days of age (King, 1965). While in rats the iris and lens are reported to be cloudy at eye opening but clear in 2-3 days (Turner, 1935), no iris clouding has been observed in deermice. Vestal and King (1968) found that infant Peromyscus can exhibit an optokinetic response as soon as their eyes open, indicating vision is functional

at that time. Clark's (1967) study on the vestibular system is the only one available on another sensory system in deermice. Young Peromyscus leucopus first exhibited nystagmus responses to rotation at 11 days of age. There was a 50% increase in number of animals responding at 15 days of age, and the response was mature at 23 days.

The Experimental Animal, Peromyscus

Two species of Peromyscus (deermice) were the subjects of this study. The genus contains mice of varying degrees of genetic relationship living in practically all types of terrestrial habitats in North America. There are 57 species, two of the most widely distributed being P. leucopus and P. maniculatus (Hall and Kelson, 1955; Hooper, 1968). Closely related forms often differ markedly in morphology, behavior, developmental pattern and natural history. This diversity provides a basis for a comparative study of the development of visual acuity. Peromyscus is nocturnal, with an all-rod retina (Moody, 1929) and no fovea (Walls, 1967). The large body of background information available on Peromyscus enables this study to be related to other aspects of the animal's biology (King, 1968b). Finally, large numbers of these animals are available for testing, allowing an estimate of the population variability of this sensory characteristic.

The experimental subjects were Peromyscus maniculatus

bairdi, the prairie deermouse, and P. leucopus noveboracensis the white-footed mouse. Both are classified in the subgenus Peromyscus, with maniculatus in the maniculatus species group and leucopus in the leucopus species group (Hooper, 1968).

P. m. bairdi inhabits the Midwestern grasslands, primarily well drained areas with rather sparse grass plant cover. They apparently prefer more open habitats than those with denser grass growth (Howard, 1959) and are rarely if ever trapped in woodlands (Blair, 1940; Nicholson, 1941). P. m. bairdi is primarily terrestrial in its habits (Howard, 1949). Horner (1954) found bairdi to perform like other terrestrial forms in tests for semi-arboreal adaptations.

P. l. noveboracensis, although rather versatile in its habitats, primarily inhabits upland mixed hardwood forests of hickory and oak (Nicholson, 1941). It may range into lowland forests in the absence of competing species and also occurs in brushy areas (McCarley, 1963) and areas of rocky outcrops (Rainey, 1955). Blair (1940) sometimes found noveboracensis in the edges of fields around woodlots, and Nicholson (1941) indicates that they prefer nest sites near the edges of woods. P. leucopus tends to nest more often in elevated than in ground level nest boxes (Nicholson, 1941; Taylor and McCarley, 1963). This nesting tendency plus the semi-arboreal types of behavior found by Horner (1954) indicates that they are more arboreal in their behavior than P.

m. bairdi. Vision appears to be important to a scansorial animal in negotiating its environment.

Morphologically bairdi is smaller than noveboracensis. Adult bairdi range from 119 to 156 mm in total length and 10 to 24 g in weight (Burt, 1957)(male mean 18.0 g, female 16.5 g, King, 1965). Adult noveboracensis range from 141-195 mm long and weigh 12-31 g (Burt, 1957)(male mean 22.9 g, female 19.7 g, King, 1965). The eye lenses of adult noveboracensis are much heavier (female mean 27.6 mg) than those of bairdi (female mean 18.2 mg) indicating a larger lens (King, 1965). The P. m. bairdi lens is almost spherical with a ratio of minimum/maximum diameter of 0.843, and the total eye bulb weight is approximately 49 mg (from Rahmann et al, 1968). No lens shape data are available for noveboracensis. The size and shape of the eye and lens are important factors in visual acuity (Rahmann, 1967, Walls, 1967).

The two species resemble each other in their morphological development. Ages at eye opening in the mice used in this study averaged almost the same for each species (12.8 $\pm$ 1.1 days for noveboracensis and 12.9 $\pm$ 1.1 days for bairdi). Other workers have reported average eye opening ages in days for noveboracensis of 13.0 (Layne, 1968) and 13.4 (Svihla, 1932) and for bairdi 12.1 (King, 1958), 13.0 (Vestal and Huff, unpublished data) and 13.7 (Svihla, 1932). Weaning age of bairdi can be early as 18 days (King, Deshaies and

Webster, 1963) while noveboracensis can be weaned by 19 days of age (Layne, 1968). They are normally weaned by the mother sometime after 22 days of age (Svihla, 1932). Layne (1968) summarized growth data from several sources on these two species. He found that in terms of percentage of mature weight at weekly intervals the two species are equal at one week and four weeks of age with noveboracensis slightly higher at two and three weeks. In noveboracensis body weight is still increasing when lens growth levels off at 25 days of age (King, 1965).

The above data indicate a strong similarity in morphological growth in the two species during the ages covered in this study. Morphological growth may affect vision by its effect on the condition of the eye (Rahmann, 1967).

Layne (1968) reviews behavioral development in Peromyscus, and in such behaviors as righting, nipple clinging and vocalizations the two species have very similar developmental patterns. The young of the two species closely resemble each other in morphological and behavioral development, while the adult ecology and behavior patterns are very different. This indicates that the young mice may also have similar patterns of sensory development which may become different after the age of weaning and before the mice reach sexual maturity.

Data on the eyes and vision of Peromyscus are rather scarce. Some have been presented above. The eye balls are

almost spherical with wide corneas and almost spherical lenses (Moody, 1929; Rahmann et al, 1968). Moody found the ciliary process to be weakly developed and apparently poorly developed iris muscles. He considered the eye to be of seemingly fixed focus with only slight accommodation for distance. Rods are the only visual elements in the retina of P. maniculatus gracilis, and this is presumably the case for other Peromyscus species. The short focal length indicates that Peromyscus should be myopic (Moody, 1929). The retinal composition of all rods is believed by Walls (1967) to be designed more for sensitivity than acuity and to indicate that the mice should have relatively poor acuity.

Rahmann et al (1968) have the only study of visual acuity in this genus. Some criticisms of their methods have been noted above, and their results are shown in Table 1. The results do indicate the relative range of distance vision and acuity for their testing situation. While P. l. noveboracensis was not tested, the other semi-arboreal forms (P. californicus and P. m. gracilis) have slightly longer visual ranges than the more terrestrial forms (P. m. bairdi, P. floridanus, and P. polionotus). The best minimum separable visual angle for the bairdi was 54' at all three light intensities tested. Because of the small numbers and methods of manipulation, no firm conclusions can be drawn concerning the effect of distance and light intensity on size of visual angle. The two semi-arboreal groups had slightly better acuity than the terrestrial forms.

Horner (1954) in studying the climbing behavior of several Peromyscus species trained the mice to jump from one 0.7 cm diameter rod to another under dim light. Using 0.7 cm as the target size her best results would indicate a minimum visible angle of 62° at 39 cm for P. m. bairdi and 40° at 60 cm for P. l. noveboracensis. This experiment was not designed to test vision, and the ranges are primarily the result of jumping ability. While her mice did use kinesthetic cues to some extent, it seems safe to assume the mice could see at least to the other rod. On the basis of Rahmann et al (1968) and Horner's (1954) results and the assumption that a scansorial animal would need good acuity at longer distances in negotiating its habitat, it could be predicted that adult P. l. noveboracensis would show better acuity at longer stimulus distances than P. m. bairdi. However, this difference may not be evident during early development.

Peromyscus species are also responsive to light intensity, as indicated in discrimination tests by Moody (1929) and King and Weisman (1966), and activity tests (Blair, 1943; Kavanau, 1967). The mice in Blair's test became inactive when ambient illuminance was increased to 0.26 ft. candles (2.8 lux) which is very dim for human eyes. Kavanau (1967) found that activity onset and cutoff intensities usually range from 0.129 lux to 2.5 lux for mice confined to a running wheel. In Rahmann et al's (1968) experiment the

acuity of the more terrestrial forms was either not affected (P. m. bairdi) or was slightly improved (P. polionotus) by decreasing illuminance. The semi-arboreal P. californicus and P. m. gracilis had better scores at higher than at lower intensities (Table 1). The values of Rahmann et al (1968) are best individual results from the mice tested, and no definite quantitative relationship to light intensity can be determined. Presumably light levels would be higher in the grassland where P. m. bairdi is found than in forests where leaf cover is dense most of the year. For this reason a forest species such as P. leucopus should be less affected by low illuminance, but in view of Rahmann et al's (1968) results the opposite relationship could be predicted.

Aims of This Study

The general aim of this study is to describe the behavioral development of visual acuity in two ecologically different species of a common wild rodent. It is meant to be an improvement over previous comparative and developmental studies in several ways. Comparative studies of vision are usually made across broad phyletic lines (Rahmann, 1967). By comparing relatively closely related species which differ in their habitat utilization we may gain data which will be useful in studying the evolutionary effects of habitat pressures on vision.

There have been problems in the measurement and presentation of data in most developmental and comparative studies of visual acuity. The visual acuity of a species or group is often given as the minimal angle or best individual performance from the group tested, with no indication of the variation in the measure (Weymouth, 1963). Some more recent studies with small numbers of animals do indicate the variability in the response. This can be corrected by using large numbers of animals of varied parentage to provide a realistic sampling of the species being studied. Another problem of previous developmental studies (Warkentin and Smith, 1937; Ordy et al, 1965) is the exclusive use of longitudinal experimental design in which the effects of experience and development are confounded. A cross-sectional experimental design can eliminate the effect of experience in the testing situation and provides data more amenable to statistical analysis.

In most studies, both developmental and comparative, the stimulus sizes and gradation intervals are those that are most readily available commercially (i.e. measured in fourths or eighths of an inch). This practice has the effect of both limiting the precision of measurement because there are large differences in stimulus size and of creating a measurement scale with unequal divisions. In addition, the same stimulus size may be used at different distances to

provide different stimulus angles, which confuses accommodation ability with acuity. By making the differences in stimulus angles sufficiently small and of equal magnitude over most of the range, and by making comparable stimulus angles for each stimulus distance, the visual angle can be measured separately. All of these changes will allow statistical analysis of the data. Finally, by controlled manipulation of species, age, distance and light intensity in the same experiment, it will be possible to show the relationships of these variables with each other.

The specific aims of this study were:

1. To describe the pattern of development of visual acuity in P. l. noveboracensis and P. m. bairdi. The adults of the two species differ in morphology and ecology, but their young are very similar in morphological and behavior development. This study will help determine if there are differences in sensory development or at what time during ontogeny the species may begin to differ.

2. To experimentally determine the effect of stimulus distance on acuity during development. Peromyscus are apparently very myopic so that acuity should be better at the shorter distances. During early development the young mice are apparently exploring their immediate environment at short range. The short range acuity should be better earlier than the long range acuity. The leucopus are more

arboreal in their habits than the maniculatus and may need sharper distance vision in scansorial behavior. If there is a species difference in development, leucopus should have sharper vision than maniculatus at the longer distances.

3. To determine how the acuity of these nocturnal rodents is affected by the ambient level of illuminance. The available data is ambivalent. Because they are nocturnal animals with very sensitive eyes, it could be expected that their acuity would not be lessened significantly by testing at low light levels where they can still be observed by the experimenter. They may show some dazzlement and loss of acuity at higher levels. If there is a species difference, leucopus should have more acute vision at lower light levels, in part because of larger absolute eye size (determined by lens weight).

MATERIALS AND METHODS

Subjects

All mice used in this study were born and raised in the breeding colony of the Michigan State University animal behavior laboratory. All were recent descendants (first to fourth generation) of animals wild-trapped in the vicinity of East Lansing, Michigan.

One-hundred nineteen P. leucopus noveboracensis and 129 P. maniculatus bairdi were tested. Eleven of the leucopus and one maniculatus were used in 2 experimental conditions, all others being used in only one. The ranking of the scores of the second tests of these 12 mice showed no observable effect of previous testing so the results were considered independent. The total number of independent scores for each species used in the statistical analysis is 130.

The mice were housed in 6 X 6 X 11 inch long clear plastic cages with wood chips and cotton bedding. Water and food (Purina mouse breeder chow) were provided ad libitum. Subjects were kept with their parents until weaning (21 days of age) and housed as a litter afterward until testing was completed.

Apparatus

The optokinetic device used to elicit the visual

response consisted of rotatable one-meter diameter wooden disc powered through belt drive by a 1/8 horsepower reversible, variable speed electric motor (Bodine Electric Company). Concentric circular grooves were cut in the wooden disc to hold upright sheet aluminum cylinders, 51 cm high, of various diameters. The cylinders were interchangeable to permit presentation of the various stimuli at different distances. Drums of radii 20 cm and 40 cm were used primarily, with some preliminary tests run with a drum of 10 cm radius. The floor of the drum was painted flat black.

Illumination was provided by an incandescent lamp mounted in a metal reflector above the center of the drum. The light was diffused by sheets of white bond paper. Three light intensities were used: 0.4 foot-candles = 4.3 lux; 8.0 foot-candles = 86.1 lux; 80 foot-candles = 861.1 lux (conversion factor 10.764 lux = 1 foot-candle (Riggs, 1965). Illuminance levels were measured by placing the probe of a light meter (Gossen Tri-Lux Foot Candle Meter, P. Gossen Co., Erlangen, Germany) facing the light source on the subject platform in the center of the apparatus. Distance of light source, bulb wattage, and number of sheets of paper used as filters were varied to provide the desired light intensities.

The visual stimuli were interchangeable striped panels lining the metal cylinder. Twenty-six X thirty-three cm long photographs of vertical black and white stripes of equal width glued to the top portion of a 51 cm wide sheet

of heavy Kraft paper formed the panels. A panel of appropriate stripe width was constructed for each visual angle tested at each distance. The angle subtended by each stripe was calculated from the tangent formed by the distance of the stripe from the center of the drum and width of the stripe. Stripes for the 10 cm drum ranged from 35' of arc to 126' of arc in 7' increments. For the 20 cm drums stripes were used which ranged from 21' of arc to 140' in 7' increments and additional stripes subtending 231', 280' and 326' of arc. Stripes for the 40 cm drum ranged from 14' to 140' of arc in 7' increments and additional stripes of 203' and 266' of arc (Appendix 1). The lower limit in stimulus angle at each distance was determined by the smallest size of stripe which could be printed and mounted accurately. A gray paper panel was used in control trials.

Subjects were restrained on a 12.5 X 10.8 cm gray wooden platform mounted on a central shaft in the apparatus, independent of cylinder motion (Figure 1). The platform was 30.5 cm above the floor of the drum during the 20 cm distance tests and 20 cm above the floor for 40 cm tests. These heights enabled ready observation and insured that a sufficiently large amount of the mouse's visual field was filled with moving stripes to elicit a response. Narrow stripes 2.4 mm apart were glued on the platform to provide a ruled background against which movements of the subject's head could be viewed. The responses were recorded visually

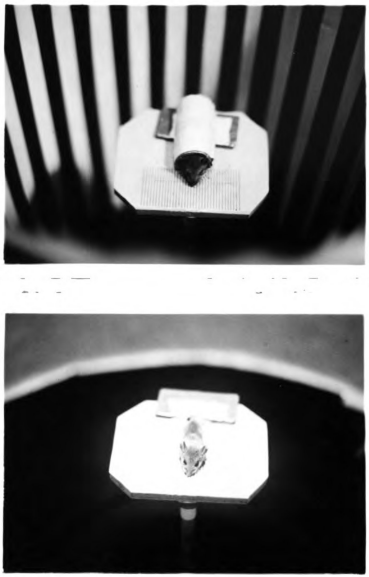

Figure 1. Mice on Platform in Testing Apparatus: Top - half-cylinder covering subject; Bottom - half-cylinder removed.

because the small size of the animals precluded using electronic recording apparatus.

Each mouse was restrained by taping its tail to a flat piece of lead. Lateral and vertical movement was restricted by a half-cylinder of lead placed over the body and resting on the platform. The head and forequarters were free to move. The center of the mouse's head between the eyes was placed over the center of the drum. However, lateral movements could carry the eyes 1-2 cm to either side of the center.

Procedures

Mice from litters of 3 to 5 young were used. Where necessary, litters were reduced to 5 young at birth. Beginning at 10 days of age litters were checked once daily for eyelid separation by applying gentle pressure to the eyelids. On the day of eye opening each mouse was toe-clipped for identification and weighed to the nearest one-tenth gram. No more than two mice from any litter were used in any experimental cell; and if two were used, they were of opposite sexes.

At the time of eye opening each litter and mouse were assigned a code number. Testing was scheduled only by code number to avoid experimenter bias. Average age at eye opening for each experimental cell is shown in Table 2, which also illustrates the overall design of the experiment.

TABLE 2 AGE IN DAYS AT EYE OPENING

Stimulus Distance		20 cm		40 cm		40 cm		40 cm	
Illuminance		86.1 lux		86.1 lux		4.3 lux		861.1 lux	
Species		Pm	Pl	Pm	Pl	Pm	Pl	Pm	Pl
Days After Eye Opening 0	Mean	12.9	12.9	13.1	13.2				
	SE	.3	.3	.3	.2				
1		12.4	13.2	13.2	12.5				
		.2	.2	.2	.4				
2		12.2	12.0	12.7	12.7				
		.5	.3	.2	.3				
3				13.5	13.3	12.7	12.8	13.1	12.6
				.2	.2	.3	.4	.3	.4
4				12.7	12.3				
				.3	.3				
5				12.9	12.6				
				.3	.2				
6				12.7	12.9				
				.4	.3				
8				13.1	12.9				
				.2	.2				

n = 10 per cell

Pm = P. maniculatus

Pl = P. leucopus

At the time of testing mice were removed from the home cage, weighed, restrained and placed in the apparatus. The mice were given 1 - 2 minutes to adapt to the light intensity. Testing began with stripes of the largest width for the distance being tested. Rotation of the drum began when the subjects were motionless or only moderately active, but apparently alert. There was no fixed inter-trial interval because it was essential to begin the trial when the mice appeared attentive. Direction of rotation was reversed for each trial. The mice responded to a wide range of rotational speeds. If subjects did not respond during the early trials, rotational speed was sometimes changed in an attempt to allow elicitation of the response.

Subjects were given eight trials of 15 seconds duration with one stripe width unless they responded earlier. An optokinetic response was recorded for either: 1. one clear head movement in the direction of drum rotation (slow phase) in which the head crossed 2 of the lines on the platform; or 2. two clear eye responses (slow and fast phases). The criterion of response to a given stripe width was an optokinetic response during at least one trial in each direction. This criterion was used to reduce effects of possible observer error.

If a mouse responded to the larger stripes, smaller stripes were inserted until the subject failed to reach criterion. Stripe size was decreased in decrements of 14'

to 28' of arc. Once the mouse failed to respond, stripe size was increased in increments of 7' of arc until the mouse responded again. The smallest stripe width to which a subject responded was designated as its minimum visual angle for the experimental condition.

Mice were observed during the intertrial intervals for head waving movements which resembled optokinetic responses. If these were seen, the subject was discarded. Mice which struggled constantly, failed to keep their eyes open, "froze" and remained immobile, or failed to respond to the largest stripes at the distance being tested were also discarded.

Six mice were tested as controls with a solid gray drum at 20 cm distance. Control tests for both maniculatus and leucopus consisted of obtaining two clear responses with a striped drum, presenting 8 trials with the gray drum, and again obtaining 2 responses with the stripes. Two observers conducted these experiments. All control mice responded to the stripes but none responded to the gray panels. The control results, the reversibility of the response, and the fact that there was a limit in the stripe size below which a response could not be elicited (a threshold) indicate that the mice were responding primarily to the experimental stimuli.

Observer reliability was calculated by the percentage of agreement between two independent observers on presence or absence of response during a trial. On 327 fifteen

second trials with 15 mice, there was 92.7% agreement between observers.

Statistical Analysis

Each experimental cell contained results from 10 subjects, 5 males and 5 females. Differences between results of experimental cells were determined by the analysis of variance and Duncan's New Multiple Range test (Li, 1964). Most data met the assumptions for these tests, except in some cases of lack of homogeneity of variance (F max-min test, Bruning and Kintz, 1968). In these cases the data were transformed to common logarithms before analysis, serving to make the results approach homogeneity of variance. Violation of this assumption would make the test more conservative by increasing acceptance of the null hypothesis (Li, 1964). Boneau (1960) finds that if sample sizes are equal, meeting the assumption of variance homogeneity is not crucial to the results of the F-test of the analysis of variance. The "t" test (Li, 1964) was used to determine the age at which 40 cm results became no different from the limit at 20 cm. Correlations of age and weight at testing with visual angle were found by the Pearson product moment correlation (Li, 1964).

The stimulus test angles were printed in intervals of 7' of arc. For the analysis the visual angles were divided by 7 to aid in calculation.

RESULTS

Pattern of Development

Preliminary tests at 10 cm stimulus distance indicated that mice of all ages consistently responded to the smallest stripe width available for that distance (35') from the day of eye opening. Accordingly, only 20 cm and 40 cm radius drums were used for the other experiments.

At 20 cm distance 95% of the mice of both species responded to the smallest stripe width presented (21') by two days after eye opening (Table 3, Figure 2). Testing was terminated at that time. The two species were not statistically different in their responses on day 0 but on day 1 leucopus' mean visual angle was significantly smaller than maniculatus'. Visual angle decreased significantly with age (analysis of variance, Table 4). P. leucopus' visual angle decreased significantly between days 0 and 1, and scores on days 1 and 2 were not different (t-test, $p > 0.05$). P. maniculatus' scores did not decrease significantly until between days 1 and 2 (t-test, $p \leq 0.05$). Mice of both species tested at 20 cm from 2 days to 6 days post eye opening consistently responded to 21' stripes.

At 40 cm distance 85% of the mice responded at the lower limit of measurement (14') on day 6, and 90% responded on day 8. The developmental patterns were similar for the two species (Table 5, Figure 3) except that maniculatus had a

TABLE 3 DEVELOPMENT OF VISUAL ANGLE AT 20 CM DISTANCE

		Days After Eye Opening		
		0	1	2
P. maniculatus	mean	63.7	60.9	21.7
	SE	6.5	11.8	0.7
P. leucopus	mean	70.7	29.4	21.0
	SE	11.1	7.6	0.0

[a] Scores in minutes of arc

n = 10 per cell

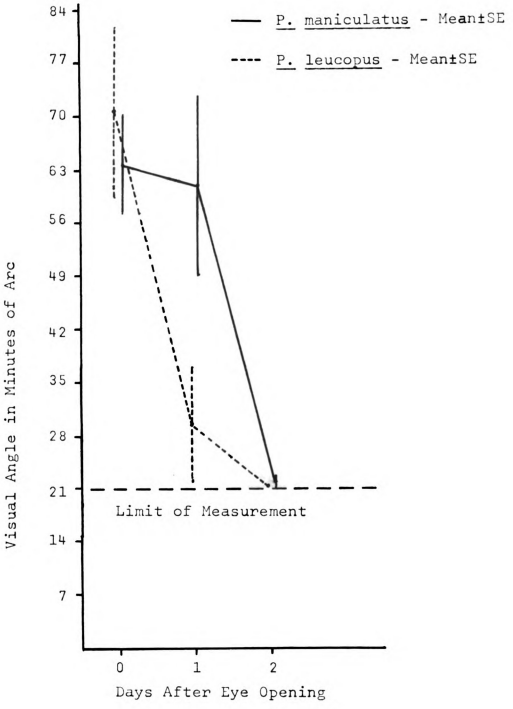

Figure 2. Development of Visual Acuity, 20 cm Distance

TABLE 4 ANALYSIS OF VARIANCE OF VISUAL ANGLE AT 20 CM DISTANCE

Source	DF	MSS	F
Day	1	99.2[a]	4.88 $p < 0.05$
Species	1	30.6	1.50
Day X Species	1	12.7	<1.
Error	36	20.3	
Total	39		

[a] Scores in visual angle in minutes/7

Species	P.leucopus	P.maniculatus	P.maniculatus	P.leucopus
Days After Eye Opening	0	0	1	1
Mean in minutes of arc	70.7[a]	63.7	60.9	29.4

[a] Means not connected by common underline are different at $p < 0.05$, Duncan's New Multiple Range Test.

TABLE 5

DEVELOPMENT OF VISUAL ANGLE AT 40 CM DISTANCE

		Days After Eye Opening							
		0	1	2	3	4	5	6	8
P.maniculatus	mean	163.0[a]	77.7	70.0	67.9	53.2	36.4	22.4	18.2
	SE	16.6	10.1	4.43	2.6	6.8	6.2	6.0	4.2
P. leucopus	mean	221.8	179.2	81.9	77.0	70.7	35.0	18.9	18.2
	SE	13.5	24.4	5.1	5.8	7.0	6.8	4.9	4.2

n = 10 per cell

[a] Scores in minutes of arc

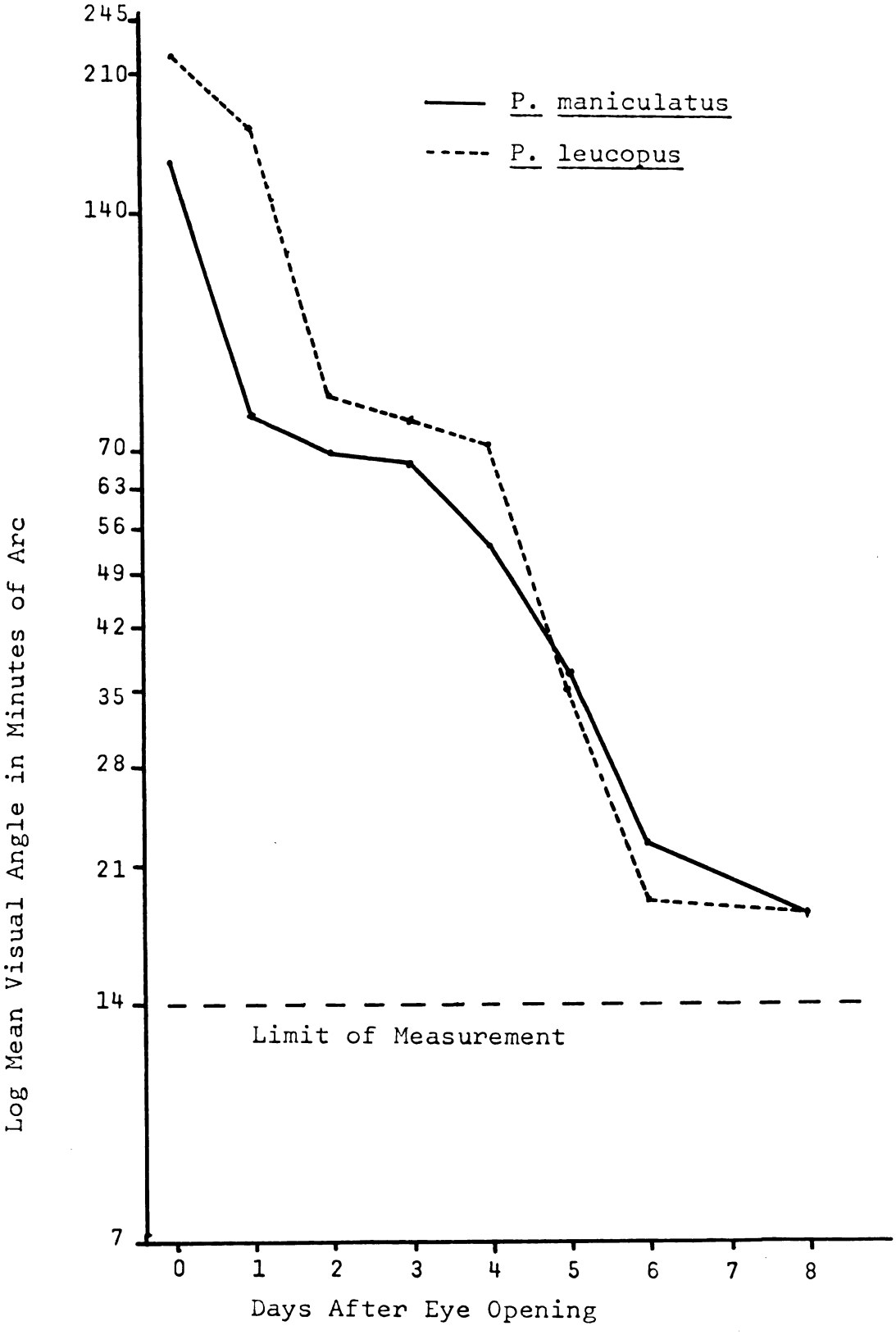

Figure 3. Development of Visual Acuity, 40 cm Distance

significant decrease in visual angle between days 0 and 1 while leucopus' scores first decreased significantly one day later (Tables 6 and 7). This relationship is the reverse of the results at 20 cm. There were significant decreases between days 4 and 5 and between days 5 and 6 in both species. The increase in weight of the experimental animals (Figure 4) was not comparable to the 9 to 12-fold decrease in mean visual angle.

Effect of Stimulus Distance

Stimulus distance had a strong effect on acuity scores in both species as indicated by the above results (Table 8). Because of the rapid decrease in visual angle to the limit of measurement at 20 cm, only results from days 0 and 1 were compared statistically between the two distances. The maniculatus 40 cm - 0 day group had a significantly larger visual angle than the other three maniculatus groups (Table 9; analysis of variance and new multiple range test, $p<0.005$). The maniculatus 40 cm - 5 day group had significantly larger visual angles than the 20 cm limit of 21' (t-test, $p < 0.05$), but the 40 cm - 6 day group was not significantly different (t-test, $p > 0.05$). Nine of the ten mice in the 20 cm - 2 day group reached the limit of 21'.

Mean visual angles of leucopus at 20 cm - days 0 and 1 were significantly smaller than the 40 cm scores (Table 10; analysis of variance and new multiple range test,

TABLE 6 ANALYSIS OF VARIANCE OF VISUAL ANGLE AT 40 CM DISTANCE

Source	DF	MSS	F
Days	7	2.822[a]	74.263 $p < 0.001$
Species	1	0.280	7.368 $p < 0.001$
Day X Species	7	0.090	2.368 $p < 0.001$
Error	144	0.038	
Total	159		

[a] Scores in $\log_{10}$ of visual angle/7

TABLE 7 SPECIES AND DAY DIFFERENCES IN MEAN VISUAL ANGLE, 40 CM DISTANCE

Species	Days Post Eye Opening	Mean
Pl[a]	0	1.493[b,c]
Pl	1	1.363
Pm	0	1.348
Pl	2	1.059
Pl	3	1.032
Pm	1	0.998
Pm	2	0.991
Pm	3	0.984
Pl	4	0.964
Pm	4	0.831
Pm	5	0.649
Pl	5	0.612
Pm	6	0.419
Pl	6	0.366
Pm	8	0.361
Pl	8	0.361

[a] Pl = *P. leucopus*; Pm = *P. maniculatus*

[b] Scores in $\log_{10}$ of visual angle/7

[c] Means not connected by common line are different at $p < 0.05$, Duncan's New Multiple Range Test

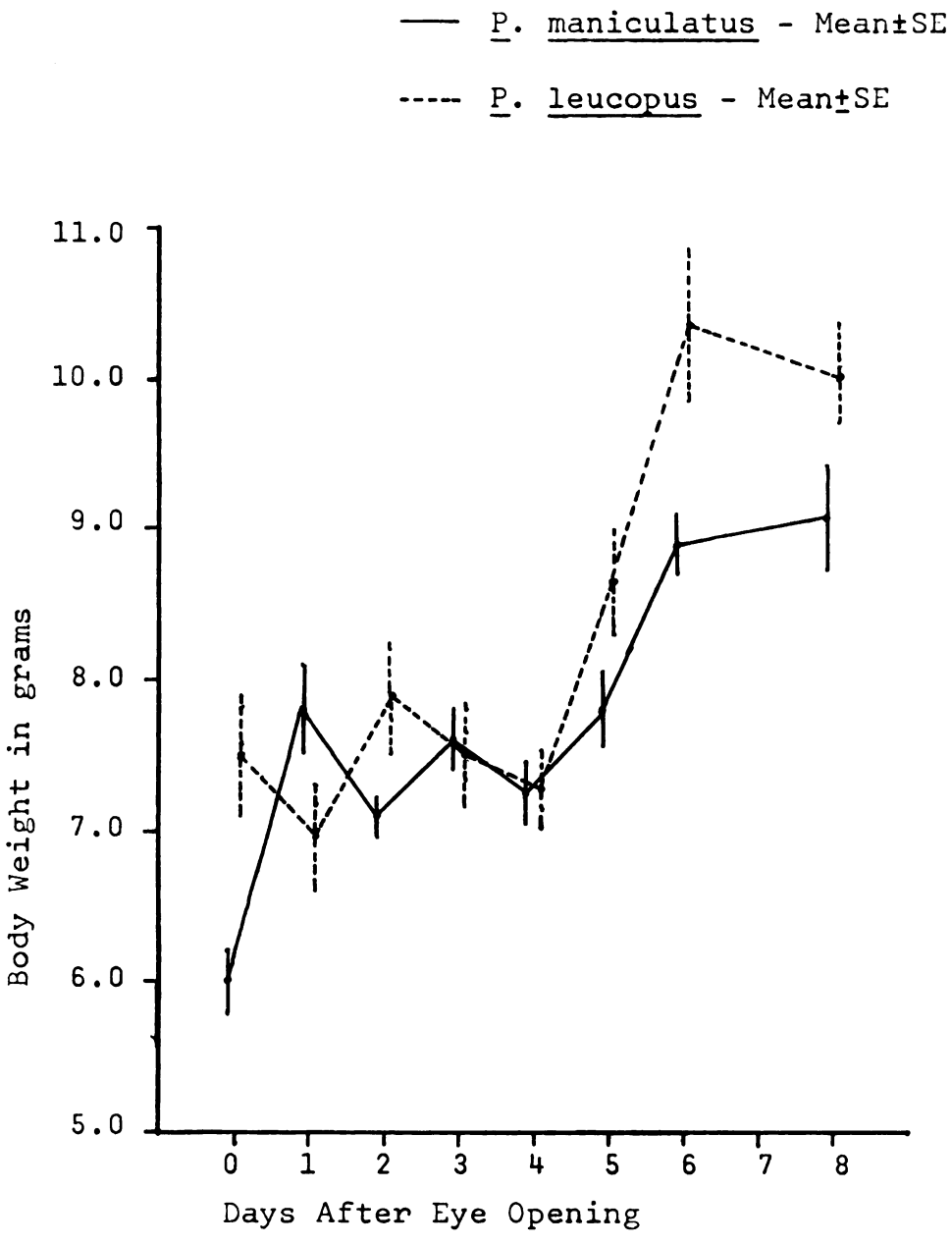

Figure 4. Weight at Time of Testing, 40cm Developmental

TABLE 8 EFFECT OF DISTANCE ON VISUAL ANGLE

Distance	Days After Eye Opening		
P. maniculatus	0	1	2
20 cm	63.7 ± 6.6[a]	60.9 ± 11.8	21.7 ± 0.7
40 cm	163.0 ±16.6	77.7 ± 10.1	70.0 ± 4.4
P. leucopus			
20 cm	70.7 ±11.1	29.4 ± 7.6	21.0 ± 0.0
40 cm	221.8 ±13.5	179.2 ±24.4	81.9 ± 5.1

[a] Mean ± S.E. in minutes of arc

n = 10 per cell

TABLE 9 EFFECT OF DISTANCE ON VISUAL ANGLE, *P. maniculatus*

Analysis of Variance

Source	DF	MSS	F
Distance	1	396.9[a]	13.9 $p < 0.005$
Days	1	688.9	24.1 $p < 0.005$
Distance X Days	1	348.1	12.2 $p < 0.005$
Error	36	28.6	
Total	39		

[a] Scores in visual angle/7

Distance and Day After Eye Opening

20 cm-Day 1	20 cm-Day 0	40 cm-Day 1	40 cm-Day 0
60.9[a,b]	63.7	77.7	163.0

[a] Mean in minutes of arc

[b] Means not connected by underline are significantly different at $p < 0.05$, Duncan's New Multiple Range test.

TABLE 10 EFFECT OF DISTANCE ON VISUAL ANGLE, P. leucopus

Analysis of Variance

Source	DF	MSS	F
Distance	1	360[a]	7.4 $p < 0.01$
Day	1	4623	94.4 $p < 0.01$
Day X Distance	1	0	<1
Error	36	49	
Total	39		

[a] Scores in visual angle/7

Distance and Day After Eye Opening

20 cm-Day 1	20 cm-Day 0	40 cm-Day 1	40 cm-Day 0
29.4[a,b]	70.7	179.2	221.9

[a] Mean in minutes of arc

[b] Means not connected by common underline are significantly different at $p < 0.05$, Duncan's New Multiple Range Test.

$p < 0.01$). The leucopus 40 cm-4 day group mean was significantly larger than the 20 cm limit of 21' (t-test, $p < 0.05$) but the 40 cm-5 day mean was not significantly different (t-test, $p > 0.05$). All the leucopus at 20 cm-2 days reached 21'.

Effect of Light Intensity

The three light intensities used in this study had no effect on mean visual angles (Table 11)(analysis of variance, $p > 0.05$). Illuminance levels lower than 4.3 lux could not be used because responses were visually recorded.

Other Variables

Because detail vision is not possible before the eyes open, the age in days after eye opening was used as the controlled variable for maturation. However, visual angle was also correlated to the chronological age at testing and weight at testing. For maniculatus the correlation was $r = -0.6924$ and for leucopus $r = -0.8240$ with chronological age ($p < 0.001$, Pearson Product Moment Correlation). The correlation with weight at time of testing was $r = -0.6203$ ($p < 0.001$) for maniculatus and $r = -0.4059$ ($p < 0.01$) in leucopus. The negative correlations correspond to the decrease in minimum visual angle with maturation. Mean values of age at testing and weight at testing for

TABLE 11 EFFECT OF ILLUMINANCE ON VISUAL ANGLE AT THREE DAYS AFTER EYE OPENING

Illuminance	*P. maniculatus*		*P. leucopus*	
(lux)	mean	SE	mean	SE
4.3	70.7[a]	3.4	63.7	6.3
86.1	67.9[b]	2.6	77.0[b]	6.3
861.1	60.9	7.7	74.9	2.1

[a] Visual angle in minutes of arc

[b] Same data as 40 cm developmental

n=10 per cell

each experimental cell are given in Tables 12 and 13 respectively.

Behavioral Observations

The experimental situation appeared to be noxious to many of the mice in that it involved restricting their movements and placing them in an exposed situation on top of a lighted platform. Approximately 13% of all the maniculatus and 6% of all the leucopus placed in the situation struggled so violently that testing was impossible for them. Of all the maniculatus placed in the apparatus 17% exhibited an immobile or"freezing" response while only 4% of the leucopus did so. While in this state the mice had their eyes open but were limp and unresponsive to such stimuli as shaking, loud noises, light flashes and electric shock. When replaced in the home cage they immediately returned to apparently normal behavior. P. maniculatus showed an increasing incidence of this response with age, ranging from 18% at 4 days up to 62% at 8 days after eye opening.

TABLE 12

DAYS OF AGE AT TESTING

Stimulus Distance		20 cm		40 cm		40 cm		40 cm	
Illuminance		86.1 lux		86.1 lux		4.3 lux		861.1 lux	
Species		Pm	Pl	Pm	Pl	Pm	Pl	Pm	Pl
Days After Eye Opening 0	Mean	12.9	12.9	13.1	13.2				
	SE	.3	.3	.3	.2				
1		13.4	14.2	14.2	13.5				
		.2	.2	.2	.4				
2		14.2	14.0	14.7	14.7				
		.5	.3	.2	.3				
3				16.5	16.3				
				.2	.2				
4				16.7	16.3	15.7	15.8	16.1	15.6
				.3	.3	.3	.4	.3	.4
5				17.9	17.6				
				.3	.2				
6				18.7	18.9				
				.4	.3				
8				21.1	20.9				
				.2	.2				

n = 10 per cell

Pm = P. maniculatus

Pl = P. leucopus

TABLE 13 WEIGHT (g) AT TIME OF TESTING

Stimulus Distance		20 cm		40 cm		40 cm		40 cm	
Illuminance		86 lux		86 lux		4.3 lux		861 lux	
Species		Pm	Pl	Pm	Pl	Pm	Pl	Pm	Pl
0	Mean	6.76	7.59	6.03	7.49				
	SE	.24	.28	.22	.38				
1		6.94	7.61	7.80	6.96				
		.23	.28	.28	.34				
2		6.65	8.25	7.09	7.88				
		.24	.22	.13	.36				
3				7.60	7.50	7.69	8.58	7.42	8.04
				.19	.34	.46	.39	.27	.28
4				7.24	7.27				
				.22	.25				
5				7.81	8.64				
				.24	.34				
6				8.90	10.35				
				.20	.49				
8				9.08	10.03				
				.36	.33				

n = 10 per cell

Pm = P. maniculatus

Pl = P. leucopus

DISCUSSION

Both species had an unexpectedly small visual angle at a relatively early age. The mean of 18.9' of arc of leucopus at 6 days and the mean of 18.2' of both species at 8 days is smaller than any visual angle yet reported for a rodent (Rahmann, 1967). Nine of 10 mice of both leucopus and maniculatus responded to 14' angles at 8 days after eye opening. Since the species values in the literature are usually the best result of any individual of that species, the 14' value indicates much better acuity than other rodents. An alternative explanation is that this testing method is more sensitive than others which have been used. Because almost all of the mice in the terminal age groups responded at the equipment limits of 21' at 20 cm and 14' at 40 cm, it seems safe to postulate that the adult threshold visual angle of these two species is smaller than 14'.

One of the criticisms of the optokinetic method has been its relative insensitivity for animals with retinal foveas. Part of this criticism may be justified but much of it may be due to the labor and difficulty involved in constructing suitable test stimuli for this response. This method appears to be at least more sensitive than the simultaneous discrimination method of Rahmann et al(1968) for Peromyscus. This is in spite of the indication that at least in human beings, acuity is lower for single moving objects than for non-moving stimuli (Ludvigh, 1948). Peromyscus appear to

be very responsive to movement. Perhaps because of their sensitivity to movement the mice were more attentive to the moving stimulus. In addition, the optokinetic response is reflexive while discrimination requires a more general voluntary body response. By eliminating the factors associated with the more general response, a closer approximation of the threshold of acuity may be reached.

The effect of stimulus distance was great enough to produce a different pattern for each distance. At 10 cm both species responded to the smallest stripe available (35') from the day of eye opening. In the 20 cm tests both species reached the limit of 21' by 2 days after eye opening. There was a significant decrease in leucopus' mean visual angle between day 0 and day 1, one day earlier than for maniculatus. At 40 cm the first significant decrease in scores occurred at the same time, but maniculatus' decreased one day earlier than leucopus'. From day 2 the curves were essentially parallel, and corresponding days were not significantly different through 8 days after eye opening. The difference in order of decrease at the two distances on day 1 may possibly be explained by slight differences in the relative ages and weights at testing of the four groups involved (Tables 12 and 13). The species groups with smaller visual angles were slightly heavier and slightly older than the groups with larger visual angles. Determination of the threshold of minimum separable acuity at maturity in these

species may contribute to the understanding of the effect of environmental selection on the pattern of visual acuity development.

The overall developmental pattern for these two species is that of more rapid development of acuity for nearby stimulus objects than for those farther away. At 10 cm distance mice of all ages could see 35' stripes. At an average of 13 days of age (day of eye opening) the mice averaged visual thresholds of 63' to 70' at 20 cm and on 2 days after eye opening (average 14 days of age) 19 of 20 responded to 21' stripes. The 40 cm group of maniculatus averaged 163' and leucopus averaged 222' thresholds at 13 days of age (day of eye opening). The pattern of change at 40 cm shows a rapid decline in mean angle from 1 to 2 days after eye opening (14 to 15 days of age), a leveling off period from 3 to 4 days (16 to 17 days of age) and then a further rapid decline in size. By 5 days after eye opening (17.6 days of age) the 40 cm leucopus average angle is not different from the day 2 average at 20 cm (21' limit), while the maniculatus 40 cm - 6 day group (18.7 days) is not different. This indicates that development of acuity at 40 cm is at least 3 to 4 days behind that for 20 cm. By 19 to 21 days of age most of the individuals of both species respond to the 14' stripe limit at 40 cm.

The adult threshold acuity values at all distances are undoubtedly better than the limiting values imposed by the

equipment limits of this experiment. Almost all mice in the terminal age groups responded to the smallest stimulus stripes available. In addition, morphological and sensory development is still going on after 19 to 21 days of age. The young mice are not normally weaned by the mother until 22 to 30 days (Svihla, 1932) and leave the home area even later (Howard, 1949). Lens weight in leucopus increases rapidly until about 25 days (King, 1965). Post-rotatory nystagmus, a response indicating vestibular system function, is mature at 23 days of age in leucopus. Adult-like habituation of this response develops even later (Clark, 1967). Peromyscus leucopus and P. maniculatus should reach the adult threshold of visual acuity by 25 to 30 days of age.

The 9 to 12 fold improvement in mean visual angle with age at 40 cm is almost certainly not due to the development of an accommodation mechanism. According to Moody (1929), Lashley (1932) and Walls (1967), rats and mice have very poorly developed ciliary muscles and fibers which would be necessary for accommodation. Walls (1967) states that small lenses have a short focal length and great depth of focus. In addition, the receptor cells are the same size as in larger eyes. This means that there will be relatively less lateral and longitudinal movement of the retinal image of a moving object than in a larger eye. Thus small-eyed animals have less need of accommodation because objects will be in focus over a longer distance. The change

in Peromyscus' visual response to stimulus distance can perhaps be explained by developmental changes in eye morphology. There may be a flattening of the shape of the lens, so that the commencement point or far point of fine focus moves out from the eye. There may be a change in the shape of the eyeball so that the focal point within the eyeball changes. A third possibility is that morphogenesis of the rods may be going on during this developmental period. DeRobertis (1956) finds that differentiation of retinal rods in white mice (Mus musculus) was complete by 12 to 16 days of age while the eyelids opened at 12 to 13 days. In his mice reorientation of the rod sacs to the adult form began in the middle of the outer rod segment and spread to either end. Tokuyasu and Yamada (1959) found that in kittens rod differentiation included elongation of the primitive rod cells followed by appearance of the primitive rod sacs first at the distal end of the cell and later development in the proximal end. If this rod elongation and differentiation is going on in Peromyscus at the ages studied in this experiment, it might cause a change in the thickness of the sensitive part of the retina. This could be a partial explanation for the change in depth of fine focus. The total effect of the interacting changes in eye morphology could account in large part for the change in depth of focus.

The distances of optimal acuity reported for rodents

range from 4 to 11 cm (Lashley, 1932; Rahmann, 1966; Rahmann et al, 1968). The visual angles of young Peromyscus at 20 cm and 40 cm are smaller than those of adult animals in the above studies. Systematic determination of adult acuity thresholds over several stimulus distances will be necessary to accurately delineate the range of fine focus in Peromyscus.

To determine the effects of light intensity, mice were tested at three days after eye opening because a true average threshold of acuity could be found at that age. The results can best be compared to Rahmann et al (1968) who used intensities of 1.08, 10.8, and 107.6 lux (see Literature Review). I used here levels of 4.3, 86, and 861 lux. The two experiments together cover a range of intensities from 1 to 861 lux but show no statistically reliable differences in response at different illuminance levels. This indicates a wide range of adaptability to light level in these nocturnal animals. We have not developed methods of adequately recording optokinetic responses when the illuminance is very low such as that under moon light (0.13 lux to 0.25 lux, Kavanau, 1967). Laboratory studies indicate that Peromyscus is most active under these very low illuminance levels (Blair, 1943; Kavanau, 1967) so that these are the light intensities under which detail vision might normally be used.

The use of days after eye opening as the indicator of

visual maturation seems well justified by the results. Age at time of testing and weight at testing are also significantly correlated with visual angle. Since all three factors are measures of maturation, this is not unexpected. Because the age at eye opening is variable and the mice cannot see before eye opening, days after eye opening still appears to be the best indicator of visual maturity for use with young mice.

The striking change in the percentage of immobility ("freezing") responses in P. m. bairdi coincides with the significant decreases in visual angle at 4 to 8 days after eye opening (17 to 21 days of age). The tendency to "freeze" in strange or noxious situations appears to be a definite subspecific characteristic of P. m. bairdi and has been noted in other experiments (King, 1961b; King, Price and Weber, 1968). King et al (1968) also note a tendency for adult P. leucopus to remain immobile in strange situations. Since the young P. leucopus in this experiment showed a low incidence of this response, the characteristic must develop later than in P. m. bairdi.

Several types of further research are suggested by the results of these experiments. The use of very narrow single lines for finding minimum visible acuity with an optokinetic device offers a means of determining the adult threshold of response and tracing the full pattern of visual acuity development in Peromyscus.

The visual system of Peromyscus is functional at eye opening but there is definite improvement in acuity and compensation for distance with increasing age. What are the relative contributions of visual experience and physical maturation to this improvement ? Vestal and King's (1968) results with the first optokinetic responses in an early eye opening strain of P. m. bairdi indicate that the opportunity for visual experience did not speed up the first appearance of the response. Once the visual system is functional however, practice may play a more important role in perceptual development. Two types of studies would bear on this problem. One is the use of deprivation experiments after eye opening to determine the effect of experience. Another is an anatomical study of development of the size and shape of the eye bulb, cornea, lens and retinal micro- and ultra-structure. The patterns of relative morphological change during the developmental period may provide the basis for the changes in acuity and visual range.

P. leucopus and P. maniculatus develop relatively good acuity at an early age. We do not yet know the age at which the mice begin to visually explore their surroundings and actually venture out of the nest. Determination of the development of early locomotory and exploratory behavior may allow predictions of the possible usefulness of this acute vision to the young mouse in its particular environment.

SUMMARY AND CONCLUSIONS

1. The best visual acuity value measured for individual P. leucopus and P. maniculatus was a minimum separable visual angle of 14' of arc at 40 cm stimulus distance. One individual of each species reached this value by four days after eye opening. The best average acuity for each species was a visual angle of 18.2' of arc at 40 cm, 8 days after eye opening. The 14' stimulus stripes were the smallest available for testing. Peromyscus has the smallest visual angle of any rodent studied to date. This result may be due to greater sensitivity of the testing method used in this experiment.

2. P. leucopus had a significant decrease in visual angle one day earlier than maniculatus at 20 cm. P. maniculatus' average decreased one day earlier at 40 cm. The differences may possibly be explained by age and weight differences between the experimental groups. The groups with smaller visual angles were slightly older and heavier than the comparable groups with larger visual angles.

3. Visual acuity improved significantly with age. The mean visual angle of maniculatus at 40 cm decreased approximately 9-fold between the day of eye opening and eight days afterward while leucopus' mean decreased approximately 12-fold. This sensory system matures at a faster rate than body weight.

4. The pattern of results during development was significantly affected by stimulus distance. At 10 cm distance all mice responded to the smallest stimulus of 35' of arc on the day of eye opening. At 20 cm 19 of 20 mice reached the 21' limit by 2 days post eye opening. At 40 cm 17 of 20 individuals reached the limit of 14' by 6 days after eye opening. Acuity for stimuli at 20 cm develops earlier than for stimuli at 40 cm.

5. Mean visual angles of both species at 3 days after eye opening were not significantly different under illuminance levels of 4.3 lux, 86.1 lux and 861.1 lux. All developmental tests were conducted under 86.1 lux. These nocturnal animals exhibit a wide range of adaptability to light intensity level.

6. Size of visual angle was significantly and negatively correlated with body weight at time of testing and chronological age at the time of testing in both species. The number of days since eye opening still appears to be the best indicator of maturation for studies of visual development in young mice.

7. Elicitation of the optokinetic response is suitable for developmental studies of visual acuity in rodents. Use of the minimum separable task appears to be limited to very early ages, and another acuity task must be used to determine adult thresholds.

8. The frequency of occurrence of the "immobility"

response by maniculatus in the experimental situation increased with age after eye opening. P. leucopus did not exhibit this response as often as maniculatus. The response appears to mature later in leucopus than in maniculatus.

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APPENDIX

APPENDIX 1

WIDTH OF TEST STRIPES IN MM

Visual Angle	Stimulus Distance		
	10 cm	20 cm	40 cm
14'	X	X	1.6
21'	X	1.2	2.4
28'	X	1.6	3.2
35'	1.0	2.0	4.0
42'	1.2	2.4	4.8
49'	1.4	2.8	5.6
56'	1.6	3.2	6.4
63'	1.8	3.6	7.2
70'	2.0	4.0	8.0
77'	2.2	4.4	8.8
84'	2.4	4.8	9.6
91'	2.6	5.2	10.4
98'	2.8	5.6	11.2
105'	3.0	6.0	12.0
112'	3.2	6.4	12.8
119'	3.4	6.8	13.6
126'	3.6	7.2	14.4
133'	X	7.6	15.2
140'	X	8.0	16.0
203'	X	X	23.2

APPENDIX 1 (cont'd)

231'	X	11.2	X
266'	X	X	30.2
280'	X	16.0	X
326'	X	19.0	X