THE DEVELOPMENT OF OCULAR NYSTAGMUS OF VESTIBULAR ORIGIN AND AFFECTS OF EARLY ROTATORY EXPERIENCE

Thesis for the Degree of Ph. D.
MICHIGAN STATE UNIVERSITY
DAVID LEE CLARK
1967

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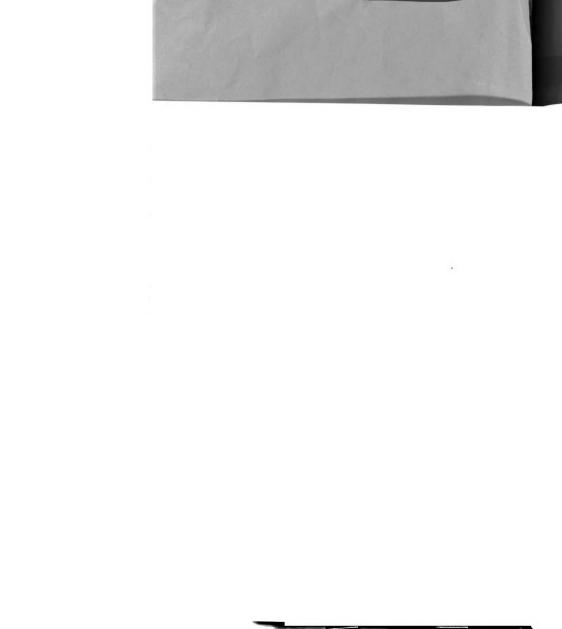
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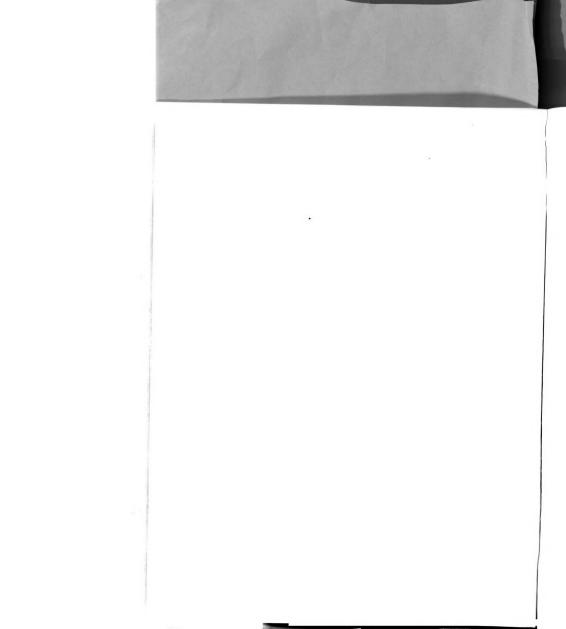


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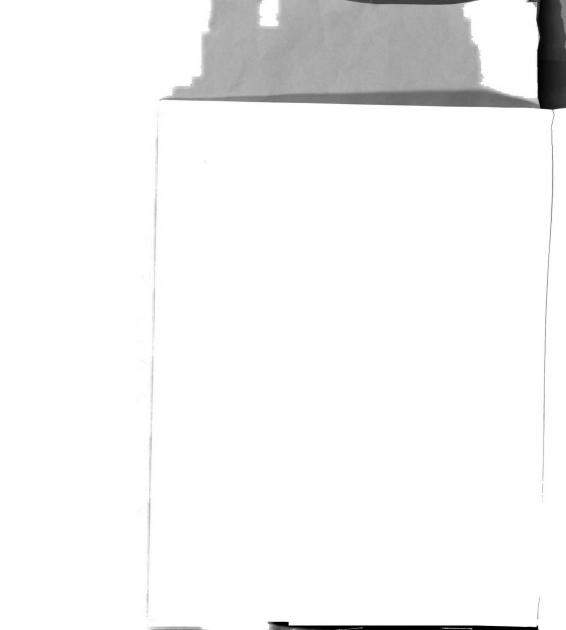
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Ву

David Lee Clark

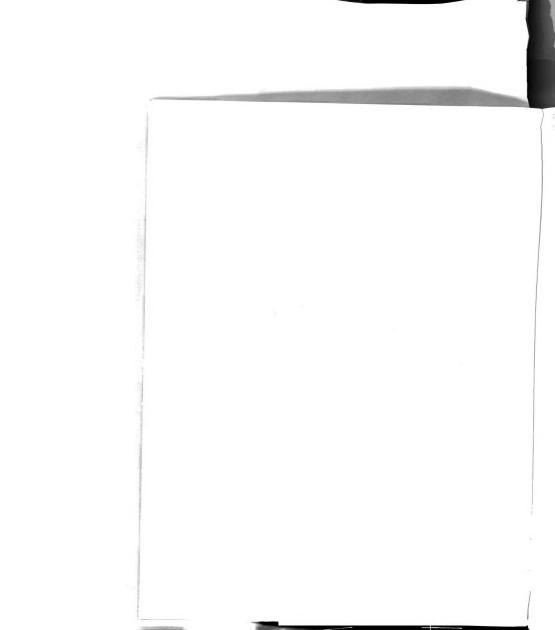
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1967









ABSTRACT

THE DEVELOPMENT OF OCULAR NYSTAGMUS OF VESTIBULAR ORIGIN AND AFFECTS OF EARLY ROTATORY EXPERIENCE

By David Lee Clark

This study was designed to answer the following questions. At what age can nystagmus of vestibular origin be first elicited in <u>Peromyscus leucopus</u>, and what quantitative changes occur in duration and cumulative of beats of post rotatory nystagmus as the response approaches maturity? Is there any differential affect on the development of nystagmus in mice tested consecutively from birth as contrasted with a new group of naive mice tested each day? Does rotational experience during the neonatal period have any affect on the nystagmus response or habituation in the adult?

The mice to be tested were mounted on a restraining device on top of a turntable. The turntable was programmed for constant acceleration and deceleration regimes. Small electrodes placed in the outer canthi of the eyes monitored the nystagmus movements of the eyes. The eye movements were permanently recorded on chart paper.

Two control groups were used. One consisted of mature mice (three months of age or older), the other consisted of mice 30 days of age. Two longitudinal developmental groups were tested. One group was tested daily from birth and the other was tested daily from 15 days of age. A cross sectional developmental group was studied from nine to 31 days of age. An experimental group received daily sessions of rotation from zero to 10 days of age



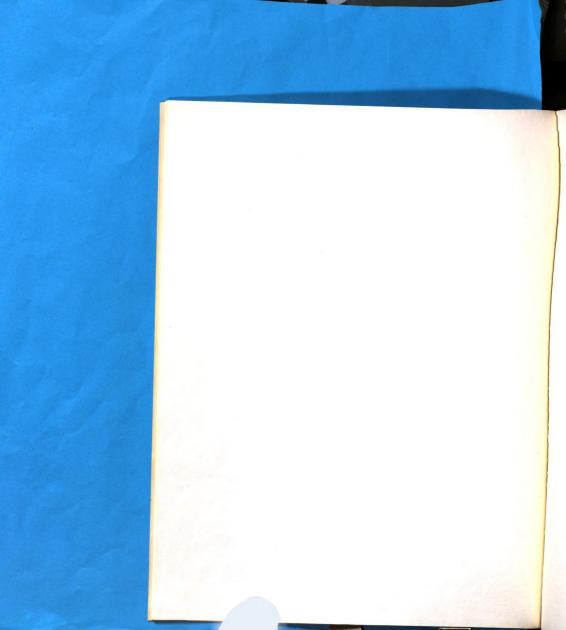


David Lee Clark

and were tested for the affects of this early experience at 30 days of age.

The data lead to the following conclusions. Post rotatory nystagmus is first seen in <u>Peromyscus leucopus</u> at 11 days of age. There is a 50% increase in animals responding at 15 days of age, and the response is mature at 23 days of age. Habituation occurs in adult <u>Peromyscus leucopus</u> and results in a response decrement of 56.5% to 62.1%. Angular acceleration experience from zero to 10 days of age has no affect on the post rotatory nystagmus, however, it results in less habituation in the adult.







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I would especially like to thank MAC (Mrs. Bernice Henderson) for her generous assistance on many technical and administrative details.

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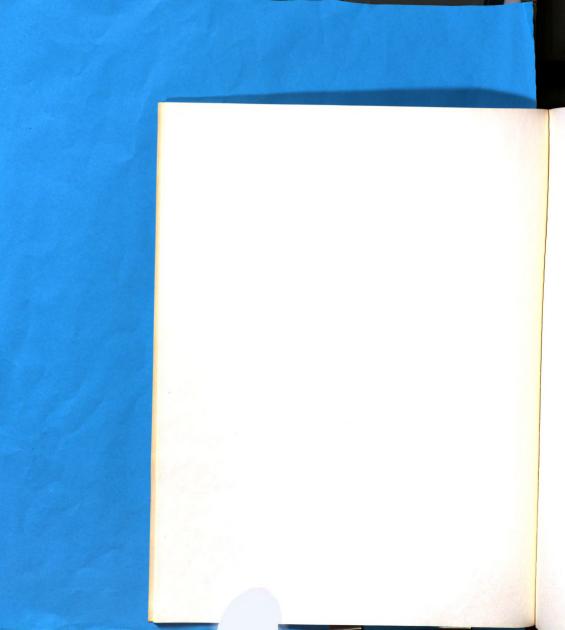
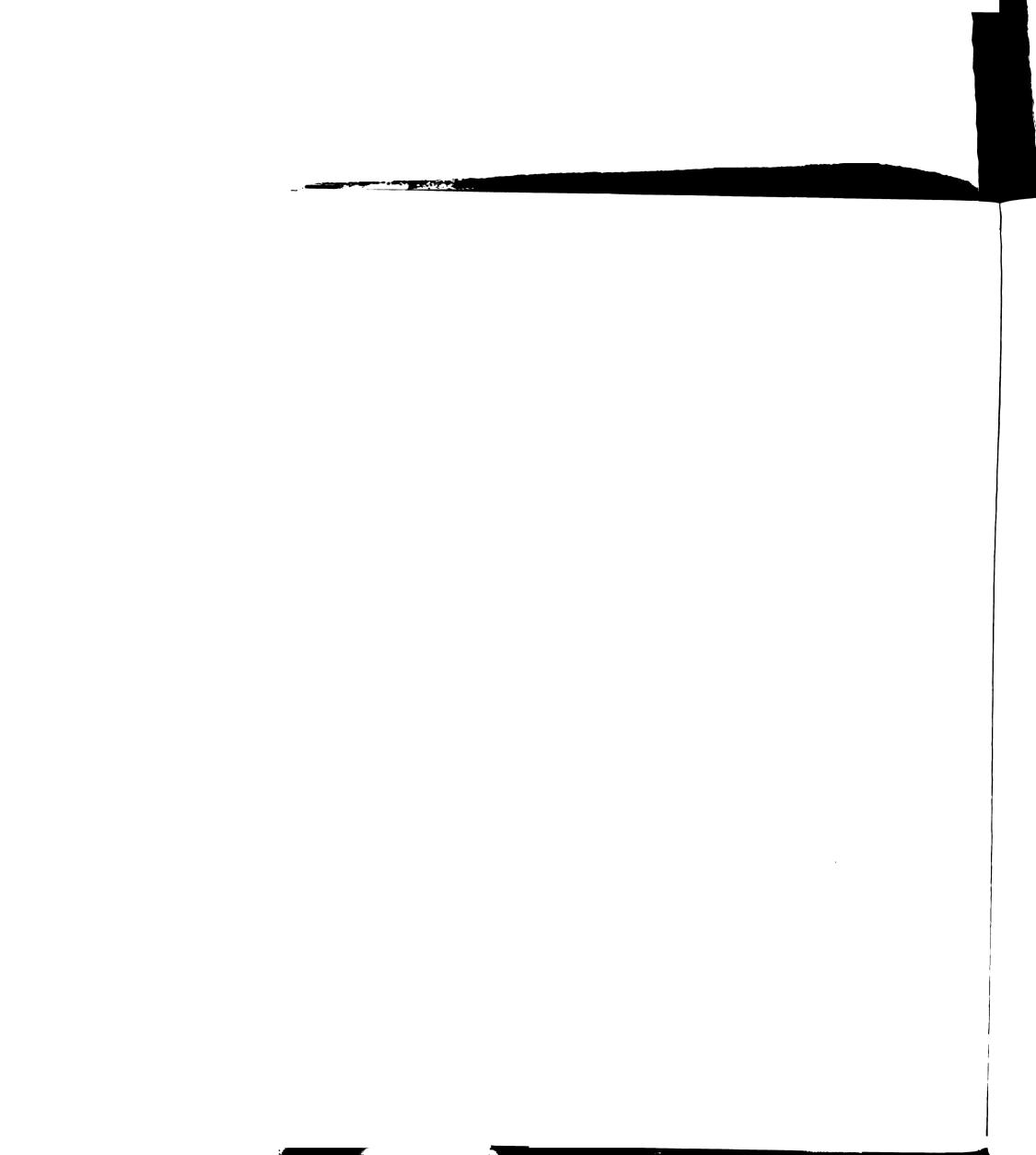




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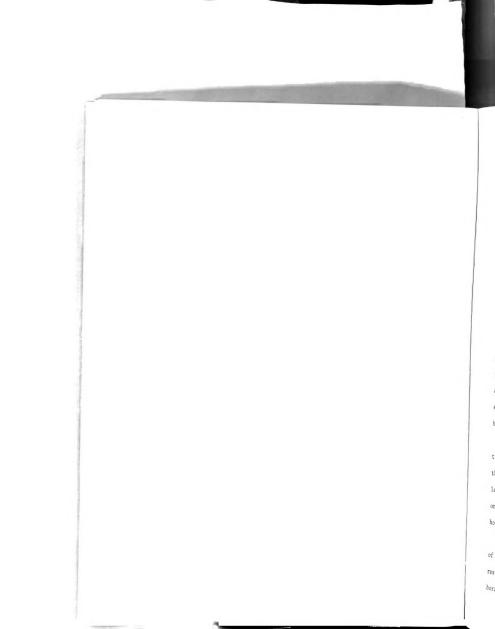


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INTRODUCTION

Nystagmus is defined as a rapid rhythmic oscillation of the eyes, usually in the horizontal plane. This oscillation is faster in one direction than in the other and nystagmus can be broken down respectively into a fast phase and a slow phase. The direction of the nystagmus beat is defined as the direction of movement of the eyes during the fast phase.

There are two sources of stimulation that produce nystagmus (other than pathological conditions such as tumors, etc.). Visual stimulation is one source, and nystagmus can be produced by rotating a vertically striped drum in front of an animal. The slow phase corresponds with visual following; the fast phase is the rapid return of the eyes. Likewise, optokinetic nystagmus can be elicited by moving an animal rapidly through an environment. This is similar to the experience one has when watching scenery pass by from a train window, hence the name; telephone pole nystagmus.

The other source of nystagmus, and the only one considered in this thesis, is vestibular stimulation; specifically stimulation of the semicircular canals. These sense organs respond to angular acceleration. Various directions of nystagmus can be produced depending on the plane of rotation, however, only the horizontal plane (and horizontal nystagmus) will be considered here.

When the head is accelerated about a vertical axis the endolymph of the horizontal semicircular canals tends to remain stationary, resulting in a deflection of the cupula, the sensory structure of the horizontal canal. Upon cessation of acceleration the cupula returns

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to an upright position due to its inherent mechanical elastic properties. The slow phase of nystagmus is generally considered to be the result of this deflection of the end organ (Camis, 1930). However, the source of the fast phase still remains a mystery. The most probable location is in the brain stem in the vicinity of the interstitial nucleus of Cajal (Bergmann, et al., 1959; Myde and Eliasson, 1957; and Lachmann and Bergmann, 1961).

During initial angular acceleration there is nystagmus resulting from the deflection of the cupula, due to the tendency of the endolymph to remain in a stationary position. This nystagmus is in the direction opposite to that of the rotation. However, if the angular acceleration ceases and a constant velocity rotation is maintained, the endolymph continues to accelerate for a short time. This causes a deflection of the cupula in the opposite direction and results in nystagmus in the same direction as that of rotation. Upon deceleration a similar series of events occurs. Initially, the animal's head decelerates more rapidly than the endolymph resulting in a deflection of the cupula opposited to the direction of rotation. The concomitant nystagmus is in the same direction as that of rotation. When the animal ceases turning, the endolymph continues to turn for a short period, deflecting the cupula in the direction the animal had been rotating. The resulting nystagmus. called post rotatory nystagmus, is opposite in direction to which the animal had been turning.

Nystagmus has not been studied comparatively and the response has been recorded in a relatively few species; the most commonly used subject is man. Some representative studies using different animals include the following: dogfish (Lowenstein and Sand, 1936), frog (Gribenski, 1964),

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The first records of nystagmus were published by Berlin (1891, cited in Dolhman, 1925). He fitted a pin onto an ivory shell which was placed on the cornea. The eye movements were recorded by the pin scratching a smoked watch glass. Another mechanical method was used by Dohlman (1925), who attached a mirror to the cornea using a rubber sucker. When the cornea moved the reflected light from the mirror was recorded on light sensitive paper. A slight improvement on this method was used by Magnus (1924) who placed small pieces of filter paper on the cornea. By photographing the eye with cinematography the nystagmus could be recorded. All these mechanical methods included one important error; the effects on nystagmus caused by the trauma of placing objects in contact with the cornea.

The first electronic recordings were made by Schott (1922, cited in Marg, 1951). He used a string galvanometer of an electrocardiograph connected to copper electrodes fastened to an eye glass frame. The electrodes were placed in the inner and outer canthus of the eye. Meyers (1929) used horseshoe-shaped tin electrodes placed on gauze saturated in saline. This was then held on the patient with bandages. Like Schott, he also used an electrocardiograph to record the eye movements. The technique was improved by Jacobsen (1930), who utilized a vacuum tube

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The first electronic teconology were wade by Webert (1922, elted in Many, 1971). Seek a status gliventement of an electroconditional connected to copies the electronic sections of an electronic section of the eye. The electronic such a status of the eye. Mayors electronic such observations in a content of the eye. Mayors ellipse that was then be if an electrocondition of the eye sections with borders. Salves, and the east of the eye sections. The electrocondition of the eye sections the eye sections. The best used an electrocondition of the eye sections. The

amplifier. Up until this time, however, the experimenter thought he had been recording action potentials of the extrinsic muscles of the eye.

Mowrer, et al., (1936), discovered that the tracings were caused by the movement of the corneoretinal potential rather than by muscle action potentials. They noted that while eye movements in the plane of the electrodes caused a pen deflection, eye movements at right angles to this plane caused none. They also found that passive movements of the eye (the muscles not contracting) gave identical results.

With the advent of more sophisticated electronic equipment the recording of eye movements using electronic means has become a standard technique. The latest technique reported was one devised by Powsner and Lion (1950), who amplified the potential through a direct current amplifier and recorded it on an oscillograph. At the same time, they fed the signal through an electronic differentiator which printed out the velocity of the eye movement. Thus, from one signal they were able to get both angular position of the eye as a function of time and also the velocity function. The velocity function can be further differentiated giving the angular acceleration (the second derivative of the original direct function) of the eye which is recorded on a third oscillograph.

Clinical applications are discussed by Jongkees (1949), von Bekesy (1955), Cawthorne, et al., (1956), Stahle (1958), Jongkees and Philipszoon (1959), Fukuda (1961), Atkinson (1961).

Nystagmus occurs and can be recorded during and after every bout of acceleration. Several studies have recorded nystagmus at these different times (Hood and Pfaltz, 1954; Brown, 1965; and Niven, et al., 1965).

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These studies have revealed that nystagmus is identical during any identical period of acceleration, regardless of the direction (i.e., either acceleration or deceleration). Likewise, post-acceleration nystagmus is dependent only on the rate and duration of acceleration, regardless of direction. These facts, plus the technical problems of recording eye movements while an animal is rotated, have resulted in postrotatory nystagmus being the most often measured response. For these same reasons, post-rotational nystagmus was recorded in our study and is discussed in this thesis.

Several parameters of nystagmus have been measured and discussed by different authors. The most widely used are duration and cumulative number of beats (von Egmond, et al., 1949). Other parameters used are amplitude of the beat (Crampton, 1962), frequency of the beats and, a recently introduced measure, velocity of the slow phase of the beat (Henriksson, 1955, 1956; Bergstedt, 1961; Brown and Crampton, 1964a; Crampton, 1962; von Egmond and Tolk, 1954; and Hinchcliffe, 1967). Amplitude and frequency are usually combined by multiplying one times the other. The resultant quotient has been called energy (E) (Ohm, 1929).

The duration and cumulative number of beats of postrotatory nystagmus were chosen as the dependent variables in this experiment for several reasons. First, these are very reliable measures and subject to the least amount of individual variation (Henriksson, 1956) and are most often used in the literature. Second, frequency was not used because the mean frequency does not take into account the constantly changing frequency that is typical of nystagmus. Third, amplitude and velocity of the slow phase were not used because of the lack of adequate equipment and, more importantly, because both of these

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measures require calibration prior to each trial. Since this calibration makes use of the animal's visual acuity, calibration of the young mice would be impossible when the eyes are closed and subject to error during the days following eye opening, or until visual acuity has matured.

All these measurements are in some degree of error if it is supposed that they give an indication of the subjective sensation of vertigo (Ek, et al., 1960; Guedry and Lauver, 1961). Forssmann et al., (1963), using humans, have shown that vertigo always outlasts any of these measures.

Habituation is defined as the decrease in nystagmic activity when an animal is repeatedly stimulated with angular acceleration (Crampton, 1964). Habituation is not influenced by the duration of the intertrial interval between stimulus sessions (Brown, 1965). This phenomenon was first called habituation by Abels in 1906. Since that time it has been observed in all birds and mammals studied. "Response Decline" or R.D., a term identical to habituation, was coined by Hood and Pfaltz (1954).

Early studies suggested that habituation was a permanent condition (Griffith, 1924; Lumphin, 1927) and this factor has been accepted as one of the characteristics of habituation. A recent study using humans however, has shown recovery of nystagmus in humans after about 2 weeks rest (Pfaltz and Arx, 1967).

Several factors have been shown to dramatically affect the development and retention of habituation. There is no nystagmus or habituation while under anesthesia, (Fearing and Mowrer, 1934; Hood

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Several turn we have been chern to dramationally affect the development and recention of heritaurion. There is no nyetagens on bublication while ander americals, (vertice and howers, 1934) Hood and Pfaltz, 1954; Henriksson, et al., 1961). Aschan et al., (1962), have shown that hypnotic suggestion can be used to both lengthen and shorten duration of nystagmus and also the velocity of the slow phase. Other mental states are also known to affect nystagmus (Angyal and Blackman, 1940; Lidvall, 1963). Even stomach distention and pregnancy have been shown to alter nystagmus (Pearcy and Hayden, 1928).

Although some studies have indicated that vision is an important factor in the development of habituation (Brown and Guedry, 1951; Mahoney, et al., 1957; van Eyck, 1960; Suzuki, 1961; and Caston and Gribenski, 1966). Others have found this doubtful (Proctor and Fernandez, 1963; and Guedry, 1964). Other workers claim that vision has no effect on habituation (Crampton, 1962a, b; Forssmann, 1964; and Brown and Crampton, 1966).

This controversy was partially answered by Collins, et al., in 1961. They found that mental arousal produced by their subjects performing mental arithmetic caused nystagmus to remain at a high level rather than habituating. The lack of arousal or a state of "reverie" results in a decrease in nystagmus, and a sleep-like state, in which the animals give no nystagmus response at all. In studies that followed, results revealed that arousal is more important than vision in affecting the habituation phenomenon (Collins, 1962, 1963a, 1964c, 1965; Collins and Guedry, 1962; Collins and Poe, 1962; Collins and Posner, 1963; and Benson et al., 1966).

In the study presented in this thesis the experimental room was illuminated at a constant level. Thus, although the level of arousal could not be specified at any level, this important contributing factor was held constant. The animals' behavior and nystagmus records gave

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was not a contributing factor in the results.

Either one of two methods of stimulating the semicircular canals are usually employed. One, often used clinically, is irrigation of the external auditory meatus with water which is at least 10° above or below body temperature. The belief is that the cooling or heating affects of the water causes the endolymph of the horizontal semicircular canal to flow, thus deflecting the cupula (Barany, 1906; and Kellogg and Graybiel, 1966). Nystagmus and habituation are both produced. The only reported difference in this first source, caloric stimulation, is a general depression caused by the cold water and a general excitation by warm water (Gernandt, 1943; and Fluur, 1961).

The second source of stimulation is rotatory acceleration. The physiology of this stimulus is described above. Various theoretical parameters of the physiological stimuli have been discussed by Mayne (1950, 1965). In practice, acceleration rates have varied from less than 1°/sec² (subthreshold) to over 6000°/sec² (Arslan, 1955). Although excessive acceleration rates may be well beyond the normal rates encountered in nature, the threshold at which irreversible damage is incurred is not known. Green and Jongkees (1948) suggested that sudden stopping from a velocity of 180°/sec (an acceleration of about 360°/sec²) may cause pathological changes, although histological studies have not revealed structural damage (Griffith, 1920a, 1920b; 1922; Gould, 1926; and Detlefsen, 1923, 1925). A study of the macula utriculi of the vestibular apparatus suggests that a 1-million-fold increase in stimulation may be necessary to cause ultrastructural

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Very few studies on the development of nystagmus have been reported in the literature. The first reported (Galebsky, 1928), utilized human babies as subjects. The majority of his observations were made during the first hours or days after birth and his conclusion was that nystagmus is present, in humans, at birth, and is essentially identical to that of adults. His acceleration rates were not controlled however, and no attempt was made to record the eye movements either mechanically or electronically. No mention of habituation was made.

A somewhat more revealing study was performed by Fish and Windle (1932), using kittens. They found that nystagmus first appears about six days after birth and that the development of the response is gradual, requiring about three weeks to mature to the adult level. As in Galebsky's study, no attempt was made to objectively record the eye movements, and there was no mention of habituation.

The most recently reported study is one by Groen (1963). These results are from only two pupples. One of which exhibited no nystagmus; the other died after the first day of testing. He had somewhat better luck using a single human baby, although his results added nothing to those reported by Galebsky. Although Groen (1965) used no objective recording techniques he did report habituation in the infant, saying that this inhibitory mechanism "might probably" be fully developed at

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about two months of age.

The purpose of this research was to study, in <u>Peromyscus leucopus</u>, the ontogeny of ocular nystagmus of vestibular origin and the effects of early angular acceleration experience.

METHODS AND MATERIALS

<u>Peromyscus leucopus</u>, the white-footed mouse, was chosen as the study animal. This mouse breeds readily, takes excellent care of its young, and matures in about two months.

In order to provide adequate vestibular stimulation, the animals were mounted rigidly in a restraining device on a turntable and subjected to angular acceleration. The restraining device consisted of two sponge rubber pads, between which the animal was sandwiched. The limbs were also anchored to the restraining device with strips of masking tape. The animal's head was held rigidly in a hose clamp; part of which was modified to fit into the animal's mouth as a bite bar. The movable bar of the clamp was fitted with a rubber pad and when the animal was placed in the device this movable bar was screwed down snugly onto the rostrum (Fig. 1).

The restraining device and hose clamp-bite bar were fastened to a 1/8" thick, $11\frac{1}{2}$ " square aluminum plate which, in turn, was secured to an ordinary $6\frac{1}{2}$ " diameter turntable.

The turntable was powered by a Globe Industries, Inc., 24 volt D.C. electric motor. The motor powered the turntable via a rim drive through an idler wheel-clutch.

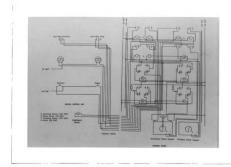
A control panel, connected to the turntable only by an electrical cable, was constructed to supply controlled D.C. current to provide

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Figure 1. Peromyscus leucopus in restraining device.



Figure 2. Schematic of wiring of electrical controls.







acceleration, constant velocity rotation, and deceleration regimes. A complete schematic of the electrical controls is presented in Figure 2. The turntable motor power supply was directly controlled by a low speed 24 volt D.C. motor connected directly to its rheostat. This control motor was, in turn, fed current by a primary power supply. This primary power supply could be set at any voltage up to 24 V.D.C.; thus determining the rate at which the power supply motor turned the rheostat on the secondary power supply. As the power supply motor turned at a constant rate this secondary power supply fed a constantly increasing voltage to the turntable drive motor. Since the rheostat on the secondary power supply was linear, the voltage increase to the turntable motor was a linear function, providing a steady linear acceleration of the turntable. A number of relays were used to automatically reverse polarity, and start and stop the turntable (Fig. 3).

In order to place an animal in the restraining device, it was first lightly anesthetized with ether. The animal was placed in a glass beaker along with an ether soaked cotton pad. This method allowed the animal to be anesthetized with a minimum of handling and struggling, while at the same time providing the experimenter full view of the animal. The animal was then placed in the restraining device. A drop of 2% Xylocaine anesthetic was administered to each eye. In the case of young <u>Peromyscus</u> whose eyes were still closed, the same electrodes were used and were placed in the same position, however, a drop of saline was applied to the skin to insure a good electrical contact.

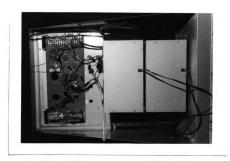


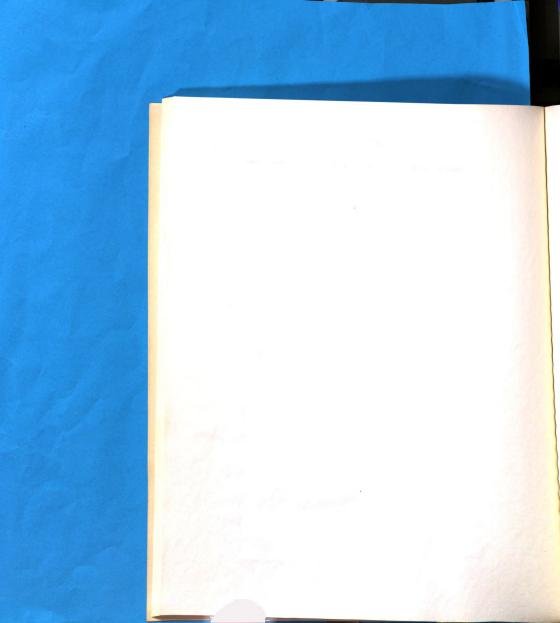


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Figure 3. Front (above) and rear (below) of control panel.





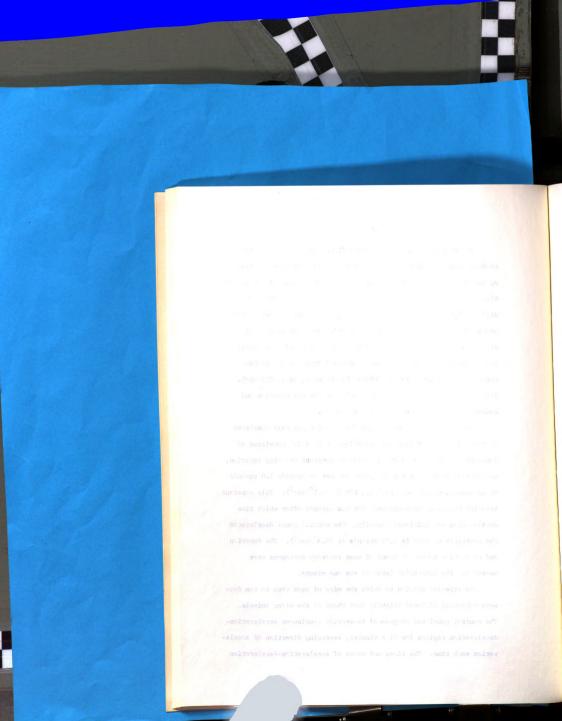


The records of the eye movements (i.e., displacement of the corneo-retinal potential) were carried from the tungsten electrodes up through a mercury swivel device (Model M-C4, Scientific Prototype Mfg., Inc., New York) and were fed into a pair of Tektronix 2A61 differential amplifiers (Tektronix Inc., Beaverton, Oregon). These amplifiers were plugged into the Tektronix 129 Power Supply which allowed us to both monitor the signal (via a Tektronix 564 Oscilloscope) and supply the signal to a Dynograph Type 542 two channel pen chart amplifier-recorder (Offner Electronics, Inc., Chicago). The paper chart records were later analyzed for the duration and number of beats of post rotational nystagmus.

Each stimulus-testing session (one session per day) consisted of ten trials of rotation and recording. Each trial consisted of constant acceleration, a short period of constant velocity rotation, and deceleration. The control panel was set to provide 5.0 seconds of acceleration from zero to 213.2 RPM (a $51.1^{\circ}/\text{sec}^2$). This constant velocity rotation was maintained for ten seconds after which time deceleration was initiated manually. The control panel decelerated the turntable to zero in 4.25 seconds (a $70.5^{\circ}/\text{sec}^2$). The duration and cumulative number of beats of post rotatory nystagmus were measured. The intertrial interval was one minute.

The stimulus session to which the mice of ages zero to ten days were subjected differed slightly from those of the older animals.

The control panel was programmed to provide continuous acceleration-deceleration regimen for five minutes, reversing direction of acceleration each time. The times and rates of acceleration-deceleration



were identical with those provided during the recording tests. The only difference for the zero to ten day animal was the absence of a ten second constant velocity period and absence of an intertrial interval.

The study was designed to answer the following questions:

I Development of Nystagmus

- A. At what age can nystagmus of vestibular origin be first elicited in <u>Peromyscus</u> <u>leucopus</u>?
- B. What changes occur in duration and cumulative number of beats of nystagmus as the response approaches maturation?
- C. At what age is the nystagmus response mature?
- D. Is there any differential affect on the development of nystagmus in mice tested consecutively from birth as contrasted with a new group of naive mice tested each day?

II Affects of Early Experience

- A. Does rotational experience during the meonatal period (day of birth until ten days of age) have any affect on the mystagmus response in the adult?
- B. Does rotational experience during the neonatal period have any αffect on habituation in the adult?

III Habituation

- A. Can habituation be demonstrated in Peromyscus leucopus?
- B. How does habituation change during development?

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I Development of Nystagmus

A group of ten adult mice (three months of age or older) were tested daily for ten days (the "Adult Control Group"). A second group, the Cross Sectional Developmental Group was made up of a total of 130 mice. Ten of these mice in the Cross Sectional Developmental Group were tested every other day from seven to 31 days of age. No mice were tested more than once. The initial day of testing of the Adult Control Group is defined as the adult response level and was compared with the Cross Sectional Developmental Group to determine the age at which the developing nystagmus response is mature. The subsequent days of testing in the Adult Control Group reveal the habituation of the nystagmus response. (See "III Habituation" below). A third group, the Zero Day Longitudinal Group was made up of twelve mice, rotated from the day of birth through nine days of age and then rotated and recorded from ten to 19 days of age. This group was to determine the development of the nystagmus response with daily sessions of rotation.

II #ffects of Early Experience

The Early Rotation Experience Group consisted of 12 mice that received rotation experience from zero through nine days of age and then were tested at 30 through 39 days of age for the nystagmus response. The results from this group were compared with the Adult Control Group and also with the 30 Day Longitudinal Group. The Adult Control Group is described above. The 30 Day Longitudinal Group is a group of ten mice tested from 30 to 39 days of age. This group allowed us to test the Early Experience experimental group at 30 days



of age using the 30 Day Longitudinal Group as a control rather than waiting for several months to elapse.

III Habituation

The Adult Control and 30 Day Longitudinal Groups provided data for habituation. A third group, the 15 Day Longitudinal Group consisted of 15 mice tested from 15 through 24 days of age. This group provided information on the development of the habituation phenomenon.

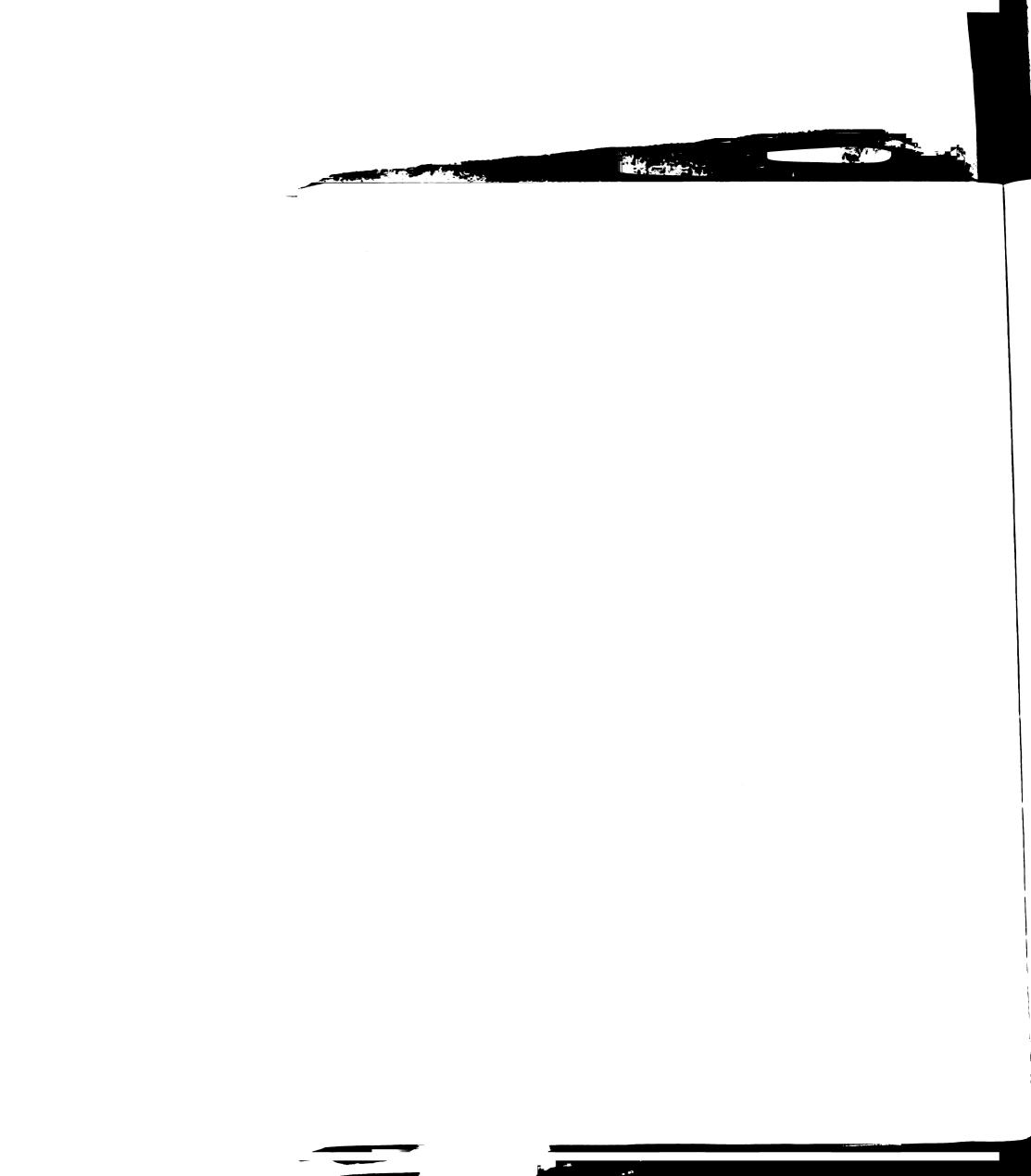
RESULTS

I Development of Nystagmus

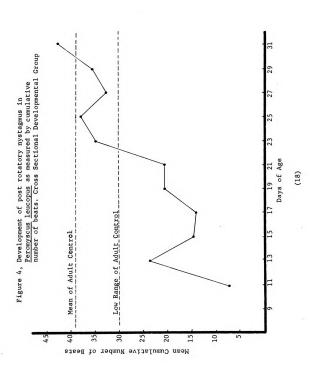
Although groups of young mice were tested regularly from seven days of age, nystagmus did not appear until 11 days of age (Figs. 4 and 5). The response continued to increase in duration and cumulative number of beats until 23 days of age, when it assumed the adult response level. In all groups tested, the direction of the fast phase of the post rotational nystagmus was opposite to the direction in which the turn-table was turning.

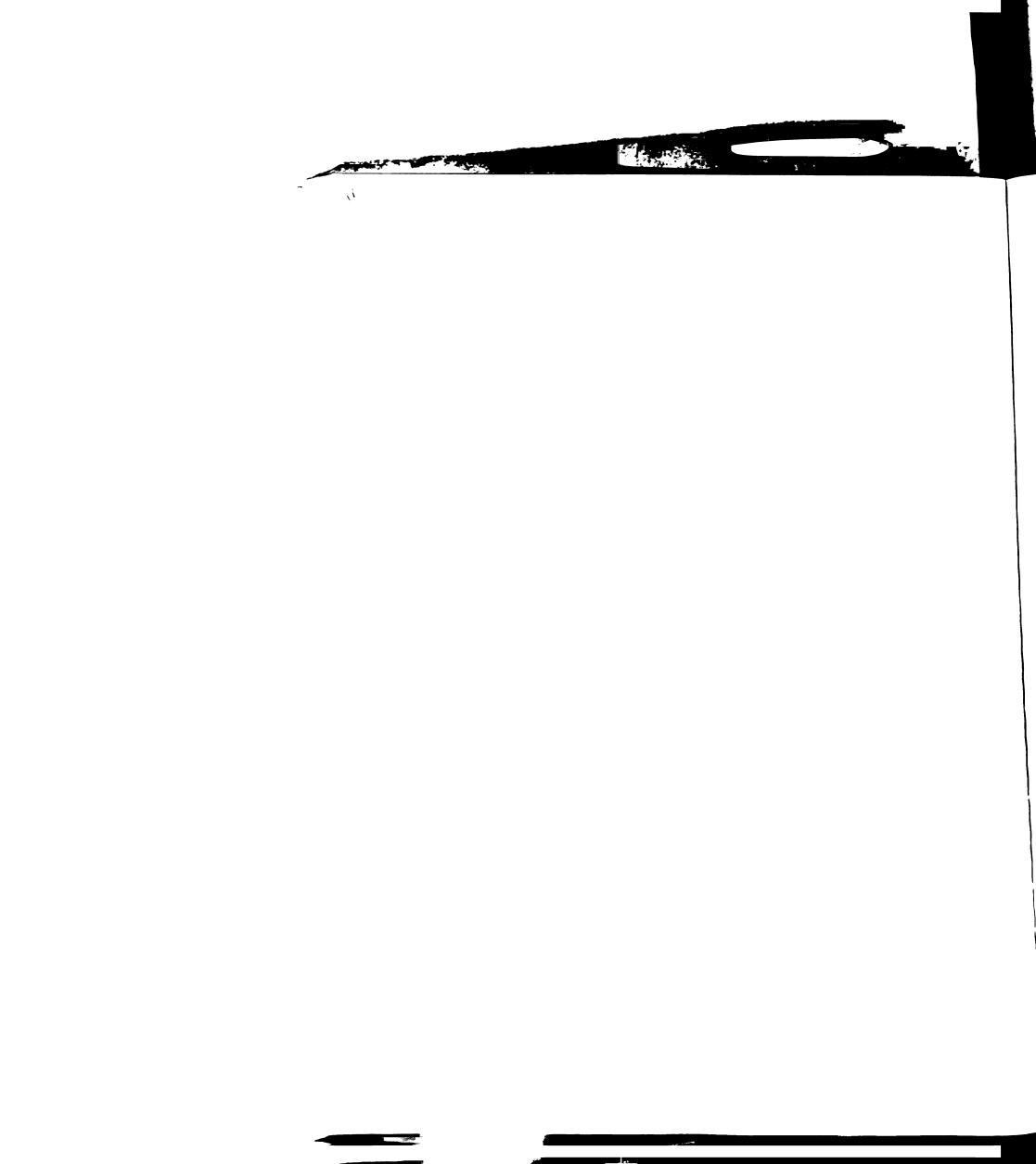
Not all animals responded at 11 days of age. Thirty per cent responded at 11 days and 20% at 13 days of age. At 15 days of age, however, the number of mice responding jumped to 70% and increased to 100% at 21 days (Fig. 6).

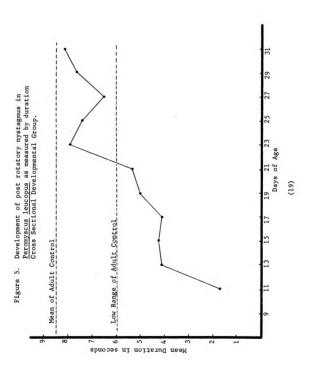
If the Cross Sectional Developmental Group is compared to the minimum level of response of the Adult Control Group (Day 1 duration of 6 seconds and cumulative beats of 30, Figs. 7 and 8), it can be seen that, of those animals responding, 80% are adult-like in response duration and 70% in cumulative number of beats at 23 days of age.

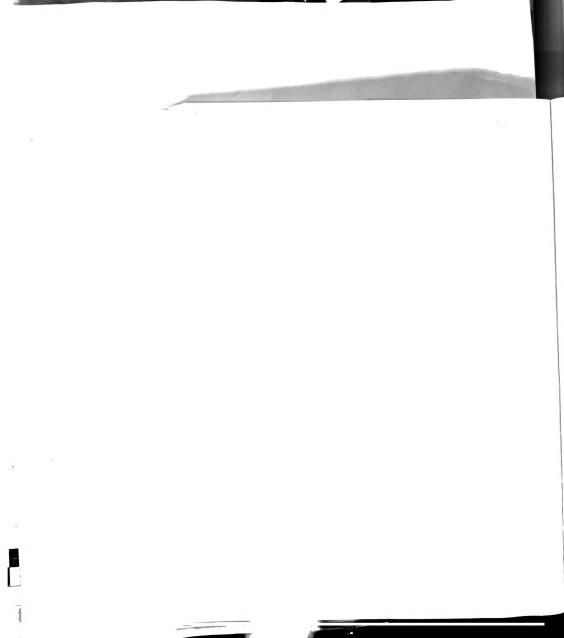






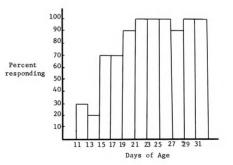


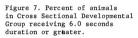


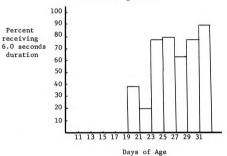


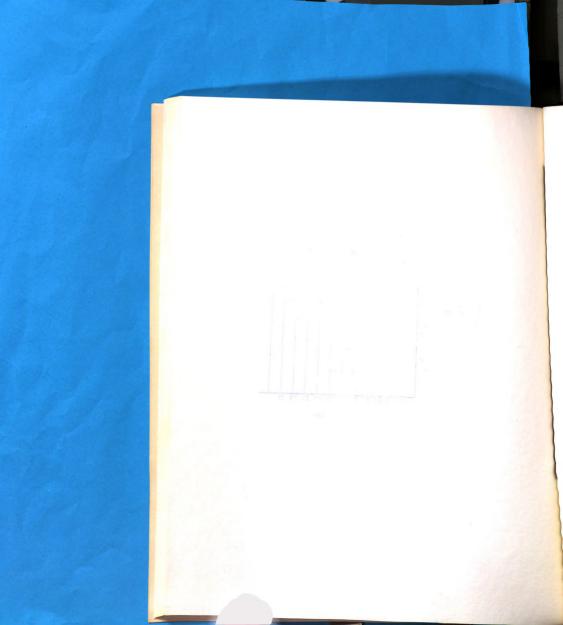
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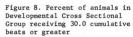
Figure 6. Percent of animals responding in Cross Sectional Developmental Group.

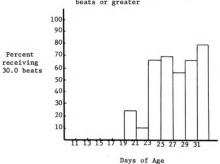


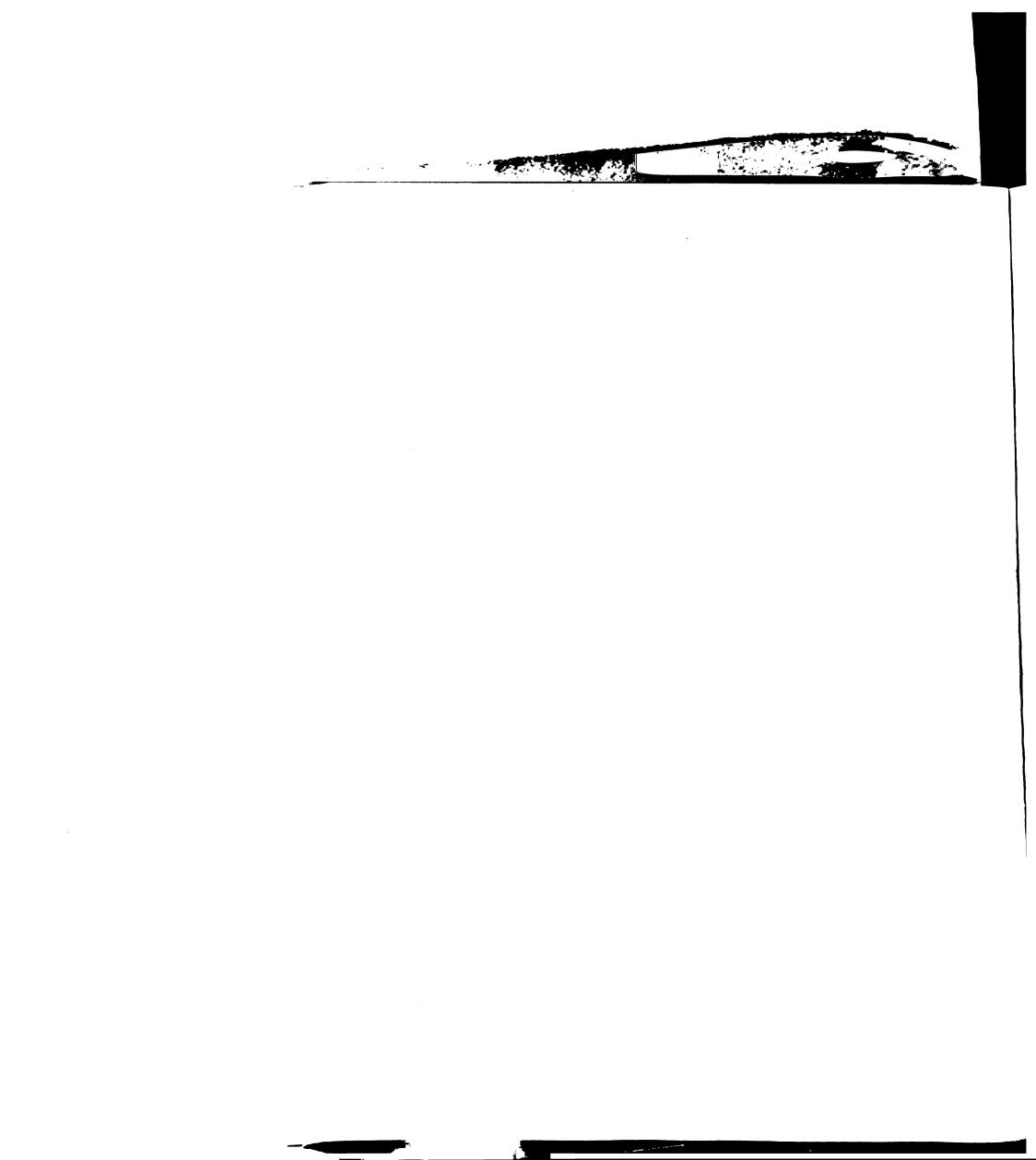


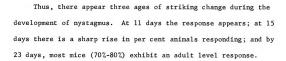












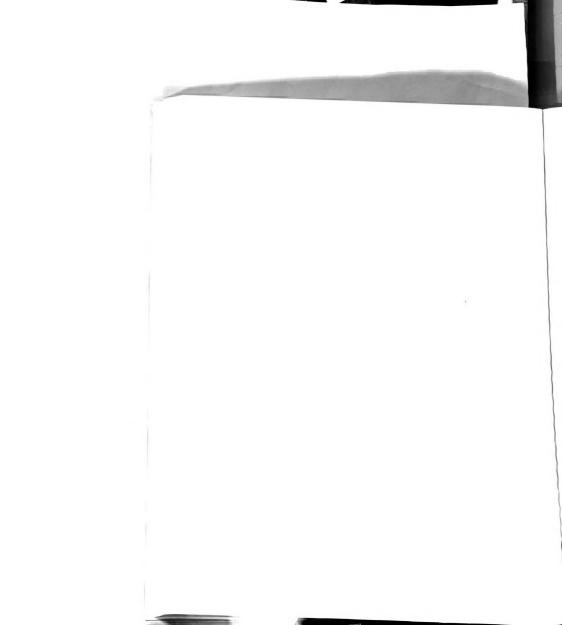
The Zero Day Longitudinal Group did not provide enough data for statistical analysis. The reason for this and the most noteworthy result from this group are that half of the mice reacted to the restraining and recording device and their responses, if any, could not be recorded. Legible records were achieved in only a few instances.

II Bffects of Early Experience

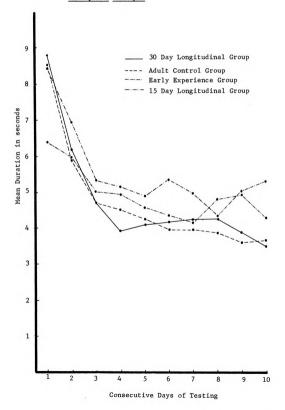
A Wilcoxan Matched Pairs test showed that the Early Experience Group, which received rotation experience from zero through nine days of age and were tested from 30 to 39 days of age, received scores which were significantly higher in both duration and cumulative number of beats when compared to both the Adult Control and 30 Day Longitudinal Groups (p<0.05Fig. 9). When the same curves were analyzed for the first day of testing, using a Mann Whitney U test, the results showed there was no significant difference. This suggests that the initial response is unaffected by early experience but that habituation of the response occurs to a lesser degree.

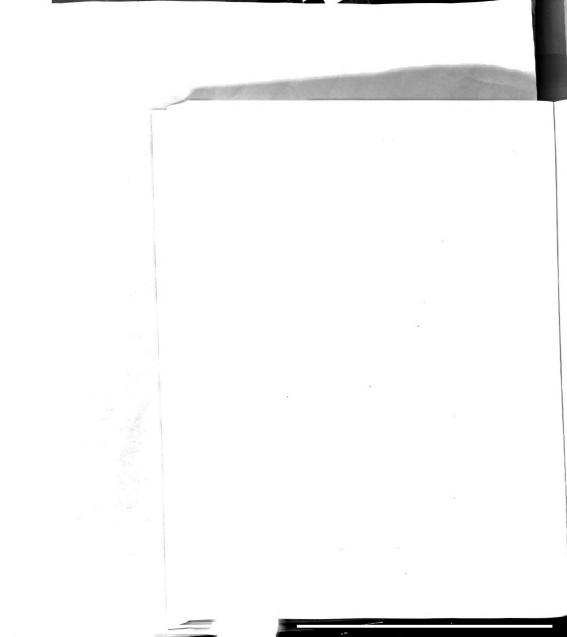
III Habituation

The response curves for the 30 Day Longitudinal Group and the Adult Control Group showed a significant drop in response over the ten day test period.(p>0.05) The 30 Day Longitudinal Group had a



(24)









59.1% drop in duration and a 68.6% drop in cumulative beats. The Adult Control Group had a 56.6% drop in duration and a 62.1% drop in cumulative beats (Fig. 10). When the curves of the two groups were compared with a Wilcoxan Matched Pairs test, the duration curve differences were not significant, however, the cumulative beat curves were significantly different (p<0.05).

As mentioned above, the Early Experience Group received scores that were significantly higher than either the Adult Control or 30 Day Longitudinal Groups.

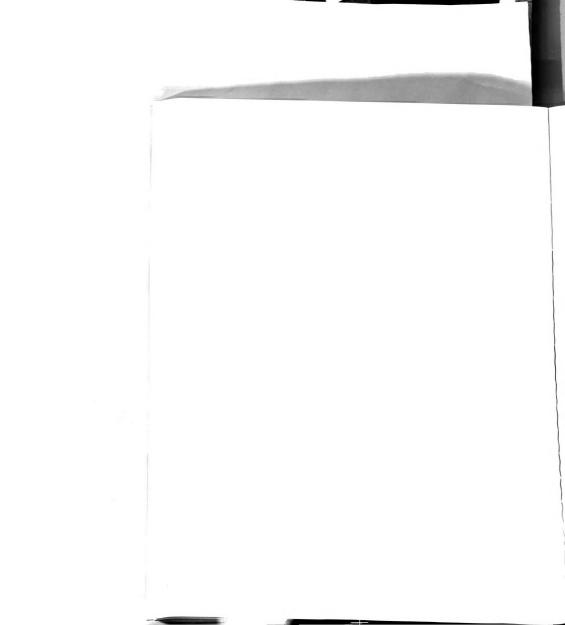
Comparing the 15 Day Longitudinal Group with the other Longitudinal groups, using a Wilcoxan Paired Scores test, showed that this curve did not differ significantly in either duration or cumulative number of beats when compared with the Adult Control Group and the 30 Day Longitudinal Group. The 15 Day Longitudinal Group, however, did receive significantly lower scores than the Early Experience Group (p<0.05). Comparing the daily scores of the 15 Day Longitudinal with the Adult Control and the 30 Day Longitudinal Groups, using a Mann Whitney U test, showed that the only day on which there was a significant difference was the first day of testing when the 15 Day Longitudinal score more closely resembled a 15 Day Cross Sectional Group score (p<0.05). Testing this first day score of the 15 Day Longitudinal against the 15 Day Cross Sectional, however, demonstrated that these two groups differed significantly (Mann Whitney U;p<0.05).

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Figure 10. Habituation of nystagmus in Peromyscus leucopus. 50 45 - 30 Day Longitudinal Group ---- Adult Control Group
---- Early Experience Group 40 ____ 15 Day Longitudinal Group Mean Cumulative Number of Beats 35 30 25 20 15 10 5 3 5 Consecutive Days of Testing



(27)

DISCUSSION

The ontogeny of nystagmus has been reported in three other mammals; the cat, dog, and human. It is difficult to compare these results with those found in Peromyscus Peromyscus Peucopus owing to the different conditions under which the response was observed. None of the studies on these other mammals reported their results in a quantitative manner and none attempted to compare cross sectional with longitudinal groups. However, a few general comparisons can be seen.

Nystagmus was first observed in Peromyscus at 11 days of age, with 70% of the mice tested responding at 15 days of age. The only comparable data were reported by Fish and Windle (1932). They found that a definite nystagmus first appeared in kittens at four days of age (6.5% of 31 kittens responded) and 74% of the same number responded at seven days of age. They also described a slow deviation of the eyes in response to rotation, on the day prior to the first nystagmus.

No slow deviation was seen in <u>Peromyscus</u>. The small size of the eyes of <u>Peromyscus leucopus</u> and the fact that we did not surgically open the eye lids prematurely, as did Fish and Windle, are contributing factors. They did not control for the surgical procedure and suggest that the opening of the eyes prematurely probably had a significant effect, hastening the development of nystagmus. These results suggest that the age of eye opening or the influence of light on the retina may be closely related to the onset of nystagmus.



(28)

Maturation of nystagmus in the mice required about 12 days from the day it first appeared. The rate of maturation was quantified in terms of the duration and the cumulative number of beats. None of the other literature reporting the development of nystagmus was quantified in any way, thus specific comparisons are impossible.

At birth, mice are at a relatively immature stage of development. The eyes and ears are closed, temperature regulation is lacking and the limbs are unable to support the body weight. Thus, it is not surprising to find the vestibular response of nystagmus absent. Both the dog (Groen, 1963) and the cat (Fish and Windle, 1932) are born in a similar condition and nystagmus is absent in both at birth. The third mammal studied, the human (Galebsky, 1928; and Groen, 1963) is born in a relatively helpless condition, however, the eyes are open and nystagmus of vestibular origin is present, although the fast component is not completely developed (Galebsky, 1928).

Development of the habituation phenomena has been discussed by Groen (1965). He suggests that, in dogs, habituation, or as he calls it, inhibition, "tends to appear at the end of the first week" of life and "after 4 weeks...is fully active." In humans, he observed that "inhibition starts to come in effectively around the 25th day to be completed after 60 days."

I Development of Nystagmus

Although Figures 4 and 5 indicate that post rotatory nystagmus commences at 11 days of age, Figure 6 points out that only 30% (or three out of 10 mice) responded at that age. The greatest increase in per cent responding is seen at 15 days of age and a one hundred

per cent response is not seen until 21 days of age. The onset of nystagmus is thus seen between 11 and 21 days of age, a range of ten days. Fifteen days of age is looked on as the mean age of onset of nystagmus as this corresponds with a response of 50% of the animals tested.

Figures 7 and 8 also point out that the development of post rotatory nystagmus takes place over a period of time. It is interesting to note, however, that there is a sudden increase in the percent of mice responding at the adult level at 23 days of age (Figs. 7 and 8). The responses chosen as parameters in Figures 7 and 8 represent the lower range of the Adult Control Group response. A response of this level or higher by the developing mice is indicative of an adult level response. (Using the mean adult level response as a criterion, would, of course, be meaningless, because the greatest possible score would be only 50%.)

Thus, there appear to be three ages at which striking changes occur in the development of post rotatory nystagmus. The response first appears at 11 days of age; there is a 50% increase in animals responding at 15 days of age; and there is a 60% increase in animals responding at the adult level at 23 days of age. Although the 11 day of age response is merely an indication of the lower limit of the age-of-response-range, the 15 day of age rise in response is the mean age at which post rotational nystagmus first appears.

The Zero Day Longitudinal Group struggled every day when put in the restraining device and gave us no quantitative data. The fact that this group responded to the testing situation in this way may be (30)

of significance but gives us no clue as to the cumulative affects on nystagmus of daily sessions of angular acceleration commencing at birth.

II Bffects of Early Experience

Since post rotatory nystagmus at 30 days of age in the Early
Experience Group was not significantly different from either the first
day of testing of either the 30 Day Longitudinal or Adult Control
Groups, there is no evidence to suggest that the adult nystagmus response
was affected by angular acceleration experience from one to 10 days of
age. However, when the Early Experience Group was tested consecutively
for 10 days starting at 30 days of age, the response curve (Figs. 9
and 10) did not drop to the same level as the control groups. That is,
the mice that received angular acceleration from one to 10 days of age
did habituate, when tested as adults, however, the response was depressed
significantly less than in the control groups.

The source of nystagmus is the vestibular sense organ, a peripheral structure. Habituation, on the other hand, is a central phenomenon (Groen, 1963,1965). Since early angular acceleration experience is affective not on the nystagmus response on the initial day of testing, but only on habituation during the following test days, it appears that the early angular acceleration experience is effective in the central nervous system and not at the peripheral sense structure. This leads us to believe that the cupula of the horizontal semicircular canal and its portion of the eighth nerve are functioning sometime prior to 10 days of age.

Preliminary histological studies, looking at the cupula and the



nerve fibers innervating it, give no evidence that any gross structural changes are occuring during the age from one to 20 days of age. (Future studies are aimed at the ontogeny of neurophysiological activity at the level of the cupula of the horizontal semicircular canal.)

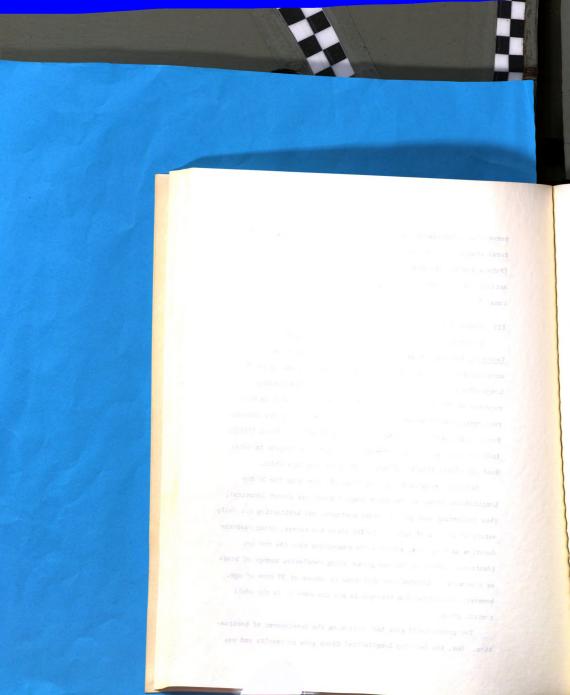
III Habituation

Habituation of post rotatory nystagmus was seen in <u>Peromyscus</u>

<u>leucopus</u> that were subjected to a series of daily sessions of angular acceleration. This response decrement was most evident in the 30 Day Longitudinal Group and the Adult Control Group. This finding was expected and the degree of habituation (about 55% to 70%) in these two control groups agrees with results published from other animals. For example, studies published by Crampton (1964), and Brown (1965), indicate a 57% to 70% reduction in post rotatory nystagmus in cats; Hood and Pfaltz (1954), indicate a 59% reduction in rabbits.

Results presented in Figures 9 and 10, show that the 30 Day
Longitudinal Group and The Adult Control Group are almost identical,
thus indicating that post rotatory nystagmus and habituation are fully
mature at 30 days of age. Comparing these two curves, using response
duration as a measure, supports the contention that the two are
identical. Comparing the two groups using cumulative number of beats
as a measure, concludes that nystagmus is mature at 30 days of age,
however, the habituation response is not the same as in the adult
control group.

Two groups would give information on the development of habituation. One, the Zero Day Longitudinal Group gave no results and was





(32)

discussed above. The other, the 15 Day Longitudinal Group, is presented in Figures 9 and 10. On the first day of testing (15 days of age) the scores fell below those of either of the 30 Day Longitudinal Group or the Adult Control Group on their first day of testing. This was anticipated since the Cross Sectional Developmental Group demonstrated that the post rotatory nystagmus response is not mature until 23 days of age. However, test scores on the 9 succeeding days (16 through 24 days of age) did not differ significantly from those on the comparable test days for the 30 Day Longitudinal Group and the Adult Control Group using both Duration and Cumulative Number of Beats. These results indicate that, although the nystagmus response is not yet mature at 15 days of age, habituation has developed completely.

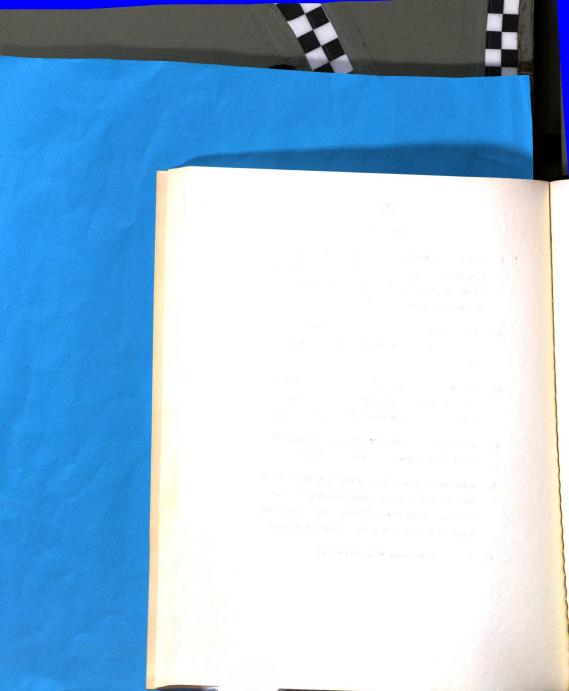
The fact that the first day of testing of the 15 Day Longitudinal Group (i.e., 15 days of age) differs significantly from the 15 day group in the Cross Sectional Developmental Group can be attributed only to sampling error.



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CONCLUSIONS

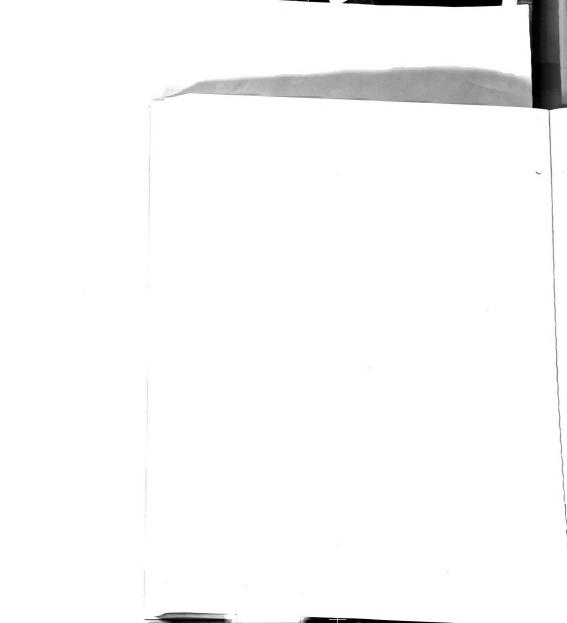
- Post rotatory nystagmus is first seen in <u>Peromyscus</u>
 <u>Leucopus</u> at 11 days of age. There is a 50% increase in animals responding at 15 days of age, and the response is mature at 23 days of age.
- Mice receiving angular acceleration experience daily from birth struggle continually when placed in the restraining device.
- Angular acceleration experience from 0 to 10 days of age has no affect on the post rotatory nystagmus, however, it results in less habituation in the adult.
- 4. Habituation occurs in adulg Peromyscus leucopus and results in a response decrement of 56.5% to 62.1%.
- 5. Measuring duration of post rotatory nystagmus leads to the conclusion that habituation is identical to the adult response in mice at 30 days of age. This is not supported if cumulative number of beats is measured.
- 6. Habituation is mature at 16 days of age.





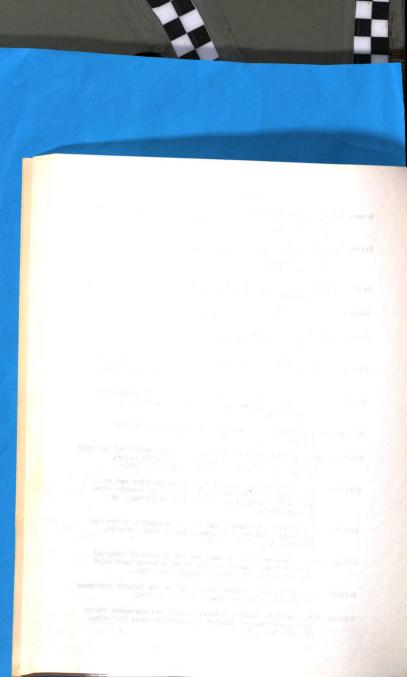
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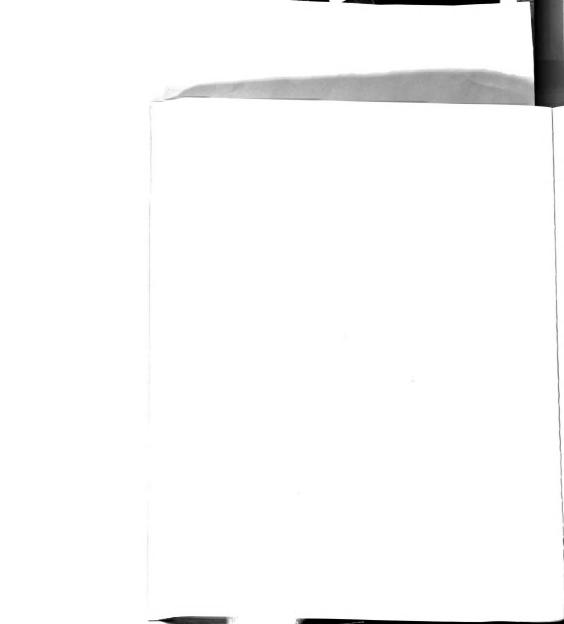
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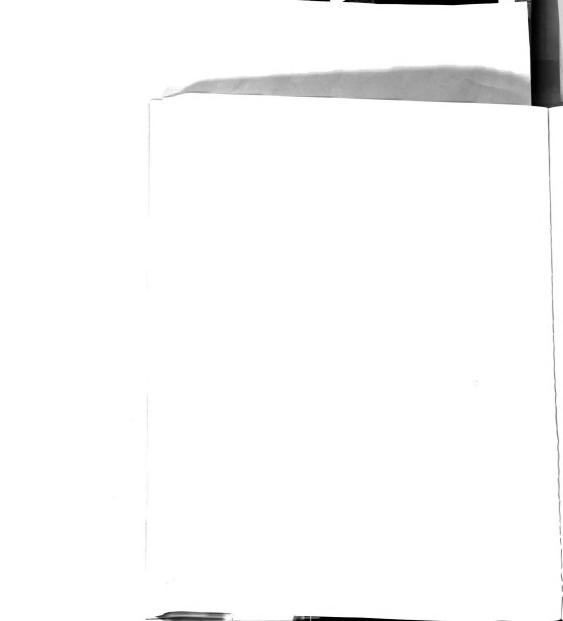
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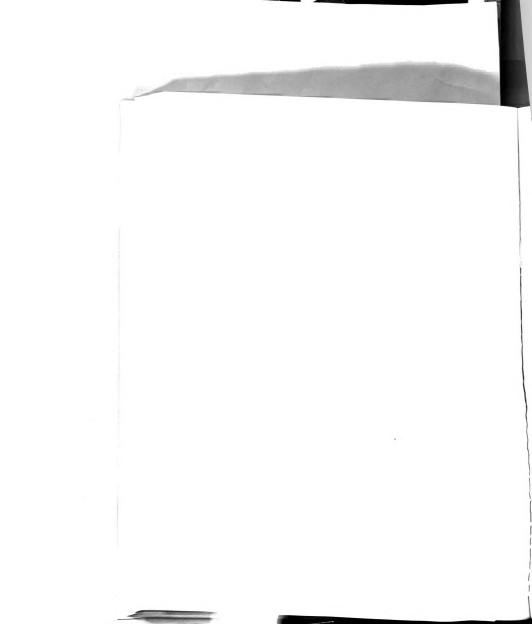
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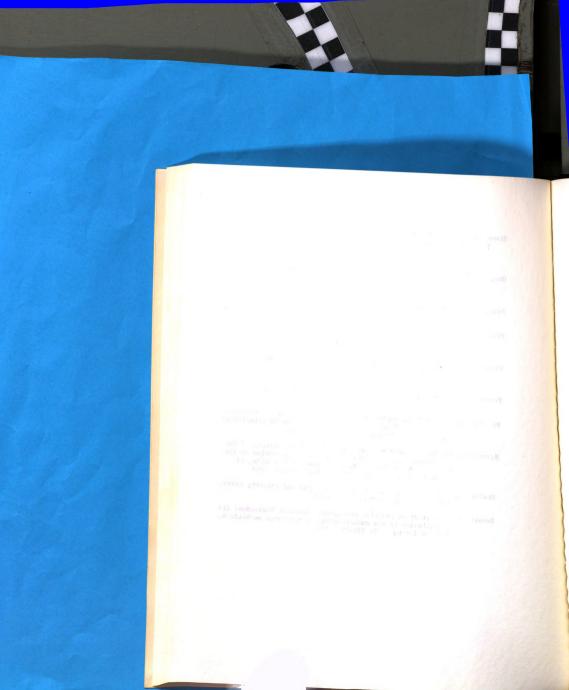
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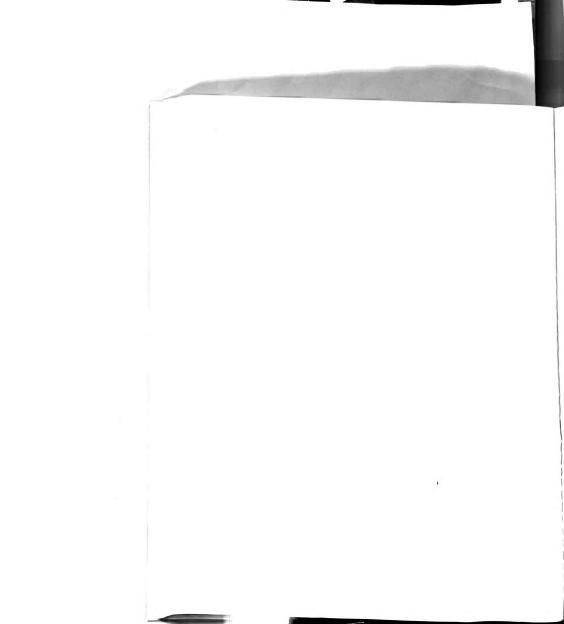


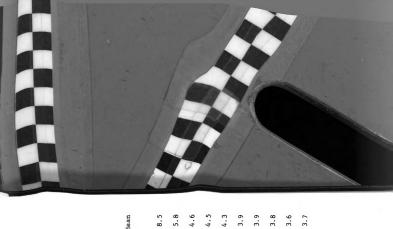
31	

APPENDEX I

		Cros	Cross Sectional Developmental Group Day of Age	al Deve	lopmenta	1 Group						
	6	11	13	15	17	19	21	23	25	27	29	31
Duration, in sec.	٠	1.7	4.1	4.3	4.1	5.0	5.3	7.9	7.4	6.5	7.6	8.1
Cumulative Number	1	7.2	23.3	14.1	13.9	20.3	20.5	34.9	37.8	32.5	36.3	42.3
			Adult	Adult Control Group	Group							
	-	2	3 243	4	5	9	7	00	6	10		
Duration, in sec.	8.5	5.8	4.6	4.5	4.3	3.9	3.9	3.6	3.6	3.7		
Cumulative Number	37.7	26.0	19.2	18.1	17.8	15.6	16.0	15.6	14.7	14.3		
			30 Day Longitudinal Group	Longitudinal	inal Gro	dn						
	1	2	8	4 4	5	9	7	00	6	10		
Duration, in sec.	8.8	6.1	4.6	3.9	4.1	4.2	4.3	4.3	3.8	3.5		
Cumulative Number	6.94	29.1	19.8	18.0	18.5	18.1	19.8	15.8	15.5	14.7		
.			15 Day Longitudinal Group	ongitud:	Inal Gro	dn						
	1	7	8	4 5	2	9	7	80	6	10		
Duration, in sec.	6.4	5.9	5.0	6.4	4.6	4.4	4.2	4.7	6.4	4.3		
Cumulative Number	25.8	22.2	18.8	18.8	17.8	17.7	17.1	20.4	21.7	18.4		
			Early E	xperienc	Early Experience Group							
	1	2	3 3	Day of Testing 4 5	sting 5	9	7	∞	6	10		
Duration, in sec.	8.4	6.9	5.4	5.2	4.8	5.4	6.4	4.4	5.0	5.3		
Cumulative Number of Beats	45.4	32.3	24.4	22.8	19.6	22.9	20.5	17.0	19.3	21.8		
				(41)		Each	n value	is the m	ean of t	Each value is the mean of ten animal's mean	l's mean	

Lacn Value is the mean of ten animal s mean scores. (I.e., each score represents 100 trials.)





APPENDIX II

Adult Control Group

5	

	A	В	O	Q	ы	ſΞŧ	9	н	I	ר	×	Me
Day of Testing												
1	•	6.9	7.2	16.9	7.1	6.4	6.9	7.5	0.9	7.6	12.0	00
2	ı	5.0	6.7	9.4	5.7	9.9		5.8	3.9	5.7	8.4	5
е	1	3.5	5.2	8.4	2.3	7.1		3.9	3.4	4.0	8.9	4
4		3.1	6.4	4.1		7.0		3.5	2.8	3.6	9.9	4
5		3.1	4.5	4.5		6.1		2.6	2.4	5.0	5.9	4
9		2.7	6.4	4.5		6.1		2.6	1.9	3.5	5.2	Э
7		2.5		9.4		5.5		3.0	2.3	3.7	5.4	ю
80		2.2		3.7		5.4		2.8	2.7	4.3	5.7	9
6		3.1		3.8		6.2		2.0	1.2	3.9	5.2	Э
10		2.1		3.8		7.2		1.8	1.4	4.4	5.4	9

(42)

Duration of Post Rotatory Mystagmus, in seconds. Each value is the mean of ten trials. NA $\,\,$ Data not available $\,\,$ = $\,$ Data not recorded $\,\,$

A			1
		1	(manager)

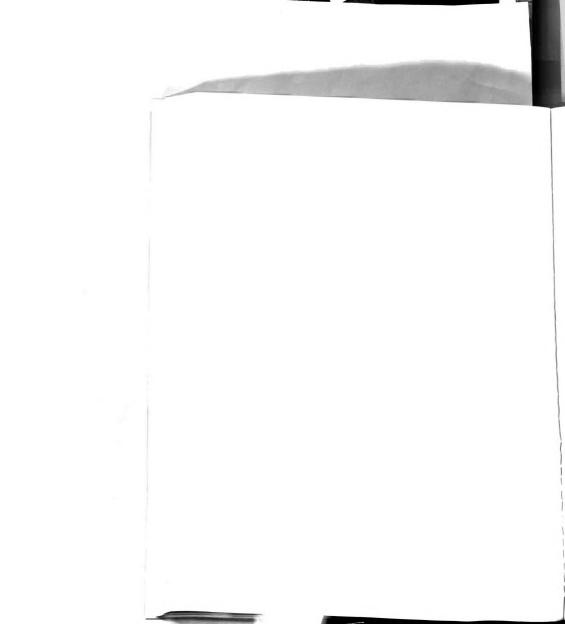
APPENDIX III

Adult Control Group

Animal Number

	A	В	O	D	ы	Į4	9	н	Ι	ר	Ж	Mean
Day of Testing												
1	-	37.7	37.9	38.8	38.1	30.4		38.6	29.6	37.1	50.9	37.7
2	ı	21.3	27.0	19.6	26.7	31.4		27.8	19.7	27.4	33.4	26.0
ဗ		12.2	19.0	19.4	0.6	34.3		17.0	14.8	19.8	27.4	19.2
4		10.6	17.4	13.2		31.9		14.5	12.9	NA	25.9	18.1
'n		10.3	15.8	20.0		28.4		6.6	9.6	25.8	22.4	17.8
9		10.8	15.9	17.5		26.6		10.7	5.6	17.5	20.0	15.6
7		9.5		19.1		23.7		13.9	8.8	17.2	20.0	16.0
8		8.9		14.3		21.1		12.0	10.8	22.2	21.3	15.6
6		8.6		14.1		26.3		6.7	5.4	18.5	21.9	14.7
10		6.3		12.7		30.5		6.3	5.0	30.7	18.5	14.3

Cumulative Number of Beats of Post Rotatory Nystagmus. Each value is the mean of ten trials. Na = Data not available = -1 bate not recorded = -1



9.4 3.9 4.1

4.3 3.8 3.5

9.4 4.3 3.9

5.0 3.7 2.9 3.4

4.0 3.5 2.8

4.5

3.4

4.2

APPENDIX IV

30 DAY LONGITUDINAL GROUP

Animal Number

Mean

	₽	p	O	Q	M	ſ×	O	н	I	
Day of Testing										
1	7.1	10.6	8.2	9.5	10.2	8.1	8.8	8.2	8.5	
2	7.4	5.2	5.4	6.7	6.4	6.3	6.4	5.7	9.9	
3		4.3	4.3	9.4	3.3	3.3	5.6	5.0	6.1	
4		3.9	8.4	2.1	3.5	3.4	3.7	5.1	5.0	
5		3.2	3.7	4.1	3.3		4.2	4.7	5.5	
9		3.4	3.8		4.0		4.3	6.4	5.0	

Duration of Post Rotatory Nystagmus, in seconds; individual mean scores. Na Data not available Na Data nor cocycled. - Bata nor cocycled.

3.9

3.7

3.3



APPENĎIX V

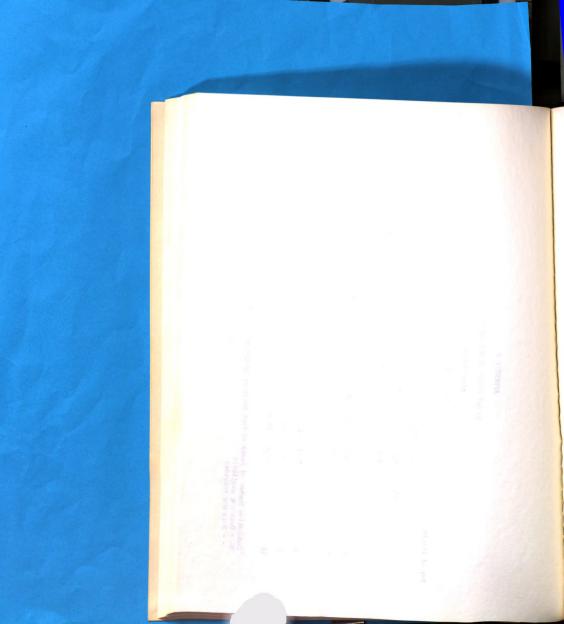
30 DAY LONGITUDINAL GROUP

Animal Number

	4	м	O	Q	ы	ĽΨ	ß	н	н	Mean
Day of Testing										
1	41.0	58.3	47.6	6.94	9.99	45.4	43.9	41.3	41.3	6.94
2	38.1	29.4	28.9	29.6	31.1	22.1	22.8	28.0	31.5	29.1
ъ		23.5	23.0	19.9	13.1	13.3	19.2	NA	26.6	19.8
4		19.6	29.3	6.9	15.3	16.0	14.0	21.7	21.2	18.0
50		16.9	16.8	21.3	15.6		13.5	20.4	24.8	18.5
9		14.7	18.6		19.4		16.1	20.5	19.8	18.2
7		14.2	30.5		19.4		16.5	18.3		19.8
80		15.7	22.8		12.9		11.4	16.3		15.8
6			26.2		9.6		10.6	15.8		15.5
10		17.6	19.9		13.6		10.4	12.2		14.7

Cumulative Number of Beats of Post Rotatory Nystagmus; individual mean scores. NA = Data not available - = Data not recorded $$(\lambda_{\rm t})$$

(42)



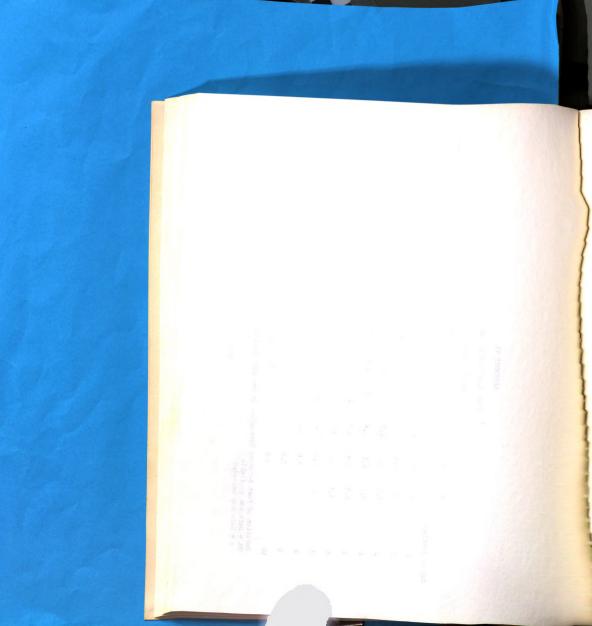
APPENDIX VI

15 DAY LONGITUDINAL GROUP

				A	Animal Number	umper						
	Ą	В	O	Q	M	Ĺ	9	Ħ	н	רי	×	Mean
Day of Testing												
1	•	3.6	6.4	•	10.0	10.7	6.3	6.2	6.1	5.7	4.6	6.5
2		4.4	6.4	1	7.0	6.9	5.9	6.2	5.8	NA	NA	5.9
٣	5.5	3.5	4.7	NA	5.2	5.6	5.0	5.0	4.1	0.9	5.5	5.0
4	5.7	6.2	4.6	4.2	3.7	4.7	5.3	5.8	3.7	•	8.4	4.9
5	4.5	5.9	4.1	2.5	5.3	6.4	4.1	5.2	3.3	5.5	6.4	9.4
9	5.7	4.7	3.7	NA	4.5	5.3	3.4	3.3			4.7	4.4
7	•	4.7	•	4.1	3.7	3.9	3.3	5.2	3.8		4.7	4.2
8		8.6	4.1	•	3.7	3.6	5.2	8.4	3.5		4.2	4.7
6		7.8			5.8	NA	2.9	5.1	3.8		4.0	6.4
10		5.8			3.9	3.8		6.4	3.3		4.3	4.3
Duration of Post Rotatory Nystagmus, in seconds; individual mean scores.	Post Rol	tatory N	ystagmus	in sec	onds; ir	ndividual	mean sco	ores.				

NA = Data not available
- = Data not recorded

(95)



	1000

APPENDIX VII

15 DAY LONGITUDINAL GROUP

Animal Number

Day

	A	В	O	Q	ы	[24	O	н	I	ח	×	Mean	
of Testing													
1	í	11.7	13.2	•	38.4	0.74	31.3	25.0	20.3	23.7	22.0	25.8	
2	•	14.7	18.0	•	27.4	27.4	20.4	27.5	20.3	NA	NA	22.2	
3	18.2	12.0	17.1	NA	19.8	21.8	21.7	21.5	14.1	26.8	17.3	18,8	
4	16.2	25.0	16.6	NA	16.3	18.4	22.0	23.4	12.2	i	19.3	18.8	
5	20.8	22.0	17.6	7.7	19.3	20.6	18.3	21.1	11.3	20.7	16.3	17.8	
9	20.0	16.8	15.5	NA	21.9	23.5	15.5	12.3	•		15.9	17.7	
7	•	16.0		17.4	16.3	15.5	13.8	24.0	14.9		18.5	17.1	
80		41.6	15.4	1	14.0	13.0	24.3	23.3	13.3		18.2	20.4	
6		37.6			26.2	NA	13.2	23.7	12.7		16.8	21.7	
10		24.1			15.5	NA		23.7	11.2		17.6	18.4	

Cumulátive Number of Beats of Post Rotatory Nystagmus; indivídual mean scores. NA = Data not available - = Data not recorded

5.2

5.4 6.4 5.0 5.3

4.4

APPENDIX VIII

EARLY EXPERIENCE GROUP

Animal Number

Mean

8.4 6.9 5.4

	A	Д	O	Q	ы	[24	9	н	Ι	ר	M	T	М
Day of Testing	**												
1	6.7	8.3	6.7	8.6	6.6	11.0	9.5	Ġ,	5.7	9.6	8.0	8.6	7.3
2	5.9	7.1	5.7	7.4	6.9	10.0	NA	NA	4.4	8.1	5.9	8.6	5.9
e	3.8	5.9	3.8	5.9	6.5	7.5	NA	5.3	3.8	0.9	4.5	6.9	8.4
4	4.2	3.8	2.9	3.9	6.4	8.2	6.7	7.7	4.0	4.9	9.4	5.4	6.4
5	3.8	2.9	3.2	3.9	3.7	6:3	5.7	4.7	4.4	7.5	9.4	6.1	5.2
9						7.1	NA	NA	3.7	9.9	9.4	5.4	5.1
7						5.5	3.8	4.8	3.8	0.9	4.3	9.9	4.0
00						5.1	8.4	4.0	3.9	3.2	NA	5.4	4.3
6						5.1	5.0	5.9		5.6	3.8	5.0	4.4
10						7.3	5.8	3.3		NA	4.0	5.5	6.1

Duration of Post Rettory Nystagmus, in seconds; individual mean scores. Na Data not available $= 1 \ \text{Data nor recorded}$

(48)



Mean	45.5	32.3	22.8	22.9	20.5	19.3	0.17	

APPENDIX IX

EARLY EXPERIENCE GROUP

Animal Number

	A	д	ပ	О	ы	Ŀ	9	н	н	Ъ	м	1	M
Day of Testing													
1	27.5	6.04	37.5	42.1	61.6	0.79	56.3		28.9	53.0	35.5	52.3	42.3
2	22.8	34.6	27.9	34.5	33.9	49.7	NA	NA	17.9	40.7	28.9	38.8	26.4
e	11.8	23.7	15.8	20.4	31.3	8.04	NA	31.9	18.4		21.9	32.9	19.7
4	11.3	16.6	12.3	14.3	19.8	44.0	29.8	43.7	15.8	26.2	21.4	23.4	18.1
5	10.9	10.4	13.0	11.6	13.0	24.5	31.0	23.4	18.0	30.0	19.1	30.2	19.1
9						32.7	NA	NA	16.0	29.4	16.2	25.0	18.1
7						24.7	21.5	28.4	12.1	22.0	13.1	29.3	12.9
80						23.1	,	NA	11.8	12.9	NA	23.1	14.1
6						23.7	NA	NA		22.4	13.7	23.6	13.2
10						30.0	32.8	12.7		NA	15.0	23.4	17.1

Cumulative Number of Beats of Post Rotatory Nystagmus; individual mean scores. NA = Data not available = Data not recorded = - α

(64)

APPENDIX X

DEVELOPMENTAL CROSS SECTIONAL GROUP

Animal Number

of Age B C D E F G H I J 9 - <th></th>												
9		A	В	O	Q	м	Œ	9	Н	н	ט	Mean
- -	Day of Age											
- 1.3 - 3.1 - 0.6 - - - - 4.8 3.4 3.0 - 3.8 - 5.5 3.8 -	6	1	•		•		٠	•	ı	1		•
- 3.2 - - 5.0 - <td>11</td> <td>1</td> <td></td> <td>1.3</td> <td>•</td> <td>3.1</td> <td>1</td> <td>9.0</td> <td>1</td> <td>,</td> <td>٠</td> <td>1.7</td>	11	1		1.3	•	3.1	1	9.0	1	,	٠	1.7
- 4.8 3.4 3.0 - 3.8 - 5.5 3.8 5.5 3.8 5.5 3.8 5.5 3.8 5.5 3.8 5.5 3.8 5.8 5.8 5.8 5.8 5.8 5.8 5.8 5.8 5.8 5.8 5.8 5.8 5.8 5.8 5.8 5.8 5.8 5.7 5.8 5.7 5.8 5.7 5.7 5.7 5.7 5.7 5.7 5.7 5.7 5.7 5.7 5.7 5.7 5.4 5.7 5.4 5.7 5.4 5.7 5.4 5.7 5.4 5.7 5.4 5.7 5.7 5.4 5.7 5.4 5.7 5.4 5.7 5.4 5.4 5.7 5.4 5.4 5.4 5.7 5.4 5.4 5.4 5.7 5.4 5.4 5.2 6.0 6.5 8.5 8.5 8.5 8.5 8.5 8.5 8.5 8.5 8.5 8.2	13	1	3.2		•	5.0			•	•		4.1
4.2 2.6 - 4.8 3.6 3.8 - 4.0 - 5.8 3.8 2.8 NA 6.2 - 3.8 6.9 3.5 4.3 8.4 8.4 8.4 8.4 8.4 8.4 8.4 8.4 8.4 8.4 8.4 8.5 8.4 8.5 8.4 8.5 8.4 8.5 <	15	1	8.4	3.4	3.0	•	3.8	•	5.5	3.8	5.5	4.3
3.8 2.8 NA 6.2 - 3.8 6.9 3.5 4.3 8.4 5.6 8.5 3.9 5.1 6.9 4.3 2.5 4.4 5.8 5.5 12.0 NA 8.2 4.3 10.5 5.0 8.8 7.6 7.7 7.4 9.7 4.9 7.1 6.4 5.1 6.5 9.0 7.2 10.6 7.4 7.4 3.4 6.0 6.7 5.4 9.1 - 5.9 NA 6.6 8.5 6.0 12.3 9.6 4.8 7.9 4.8 9.6 NA 6.2 7.3 6.9 6.7 9.0 7.1 10.6 8.2 10.1 7.3 5.7 9.3	17	4.2	2.6		8.4	3.6	3.8	•	4.0	•	5.8	4.1
5.6 8.5 3.9 5.1 6.9 4.3 2.5 4.4 5.8 5.5 12.0 NA 8.2 4.3 10.5 5.0 8.8 7.6 7.7 7.4 9.7 4.9 7.1 6.4 5.1 6.5 9.0 7.2 10.6 7.4 3.4 6.0 6.7 5.4 9.1 - 5.9 NA 6.6 8.5 6.0 12.3 9.6 4.8 7.9 4.8 9.6 NA 6.2 7.3 6.9 6.7 9.0 7.1 10.6 8.2 10.1 7.3 5.7 9.3	19	3.8	2.8	NA	6.2	•	3.8	6.9	3.5	4.3	8.4	5.0
12.0 NA 8.2 4.3 10.5 5.0 8.8 7.6 7.7 7.4 9.7 4.9 7.1 6.4 5.1 6.5 9.0 7.2 10.6 7.4 7.4 9.1 6.4 5.1 6.5 9.0 7.2 10.6 7.4 7.4 6.0 6.7 5.4 9.1 - 5.9 NA 6.6 8.5 8.5 6.0 12.3 9.6 4.8 7.9 4.8 9.6 NA 6.2 7.3 6.7 9.9 7.1 10.6 8.2 10.1 7.3 5.7 9.3	21	5.6	8.5	3.9	5.1	6.9	4.3	2.5	4.4	5.8	5.5	5.3
9.7 4.9 7.1 6.4 5.1 6.5 9.0 7.2 10.6 7.4 3.4 6.0 6.7 5.4 9.1 - 5.9 NA 6.6 8.5 6.0 12.3 9.6 4.8 7.9 4.8 9.6 NA 6.2 7.3 6.9 6.7 9.0 7.1 10.6 8.2 10.1 7.3 5.7 9.3	23	12.0	NA	8.2	4.3	10.5	5.0	8.8	7.6	7.7	7.4	7.9
3.4 6.0 6.7 5.4 9.1 - 5.9 NA 6.6 8.5 6.0 12.3 9.6 4.8 7.9 4.8 9.6 NA 6.2 7.3 6.9 6.7 9.0 7.1 10.6 8.2 10.1 7.3 5.7 9.3	25	9.7	6.4	7.1	6.4	5.1	6.5	0.6	7.2	10.6	7.4	7.4
6.0 12.3 9.6 4.8 7.9 4.8 9.6 NA 6.2 7.3 6.9 6.7 9.0 7.1 10.6 8.2 10.1 7.3 5.7 9.3	27	3.4	0.9	6.7	5.4	9.1		5.9	NA	9.9	8.5	6.5
6.9 6.7 9.0 7.1 10.6 8.2 10.1 7.3 5.7 9.3	29	6.0	12.3	9.6	8.4	7.9	8.4	9.6	NA	6.2	7.3	7.6
	31	6.9	6.7	0.6	7.1	10.6	8.2	10.1	7.3	5.7	9.3	8.1

Duration of Post Rotatory Nystagmus, in seconds; individual mean scores of individual mice. NA = Data not available

- = Data not recorded

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None Park A

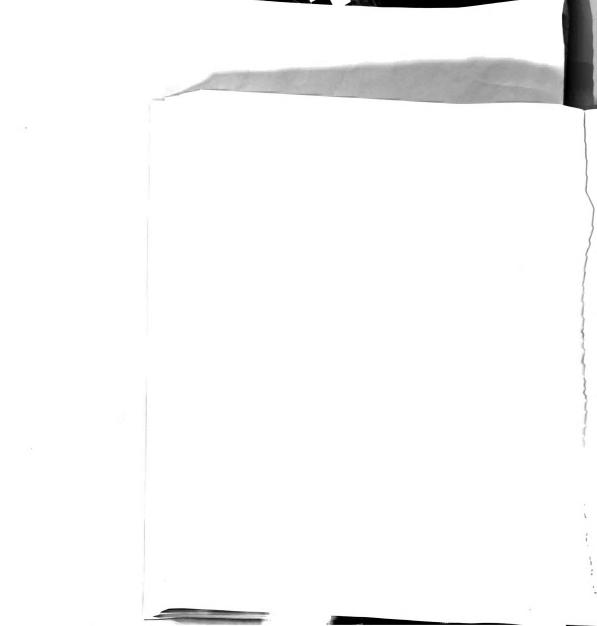
APPENDIX XI

DEVELOPMENTAL CROSS SECTIONAL GROUP

Animal Number

	А	Д	O	Д	ы	[II4	Ð	H	п	ח	Mean
Day of Age											
6	•		٠	1	r	ı	٠		1	1	·
11	•	•	2.9		16.1	1	2.7	•	1	1	7.2
13	1	22.3		ı	24.3	•			1	,	23.3
15		13.9	12.5	11.4	٠	8.6	•	16.3	16.7	18.2	14.1
17	16.1	10.2	•	16.2	10.8	14.5	ì	13.8		15.8	13.9
19	17.0	13.3	NA	20.5		12.6	36.1	12.1	17.8	33.1	20.3
21	23.2	41.9	14.0	18.0	26.1	16.5	8.6	11.0	25.6	19.6	20.5
23	55.3	NA	41.8	20.0	33.7	22.6	45.8	33.0	29.1	33.0	34.9
25	6.09	26.9	33.3	28.1	26.3	29.7	47.8	34.7	48.7	41.8	37.8
27	16.0	33.0	35.4	28.9	44.3	•	27.2	NA	NA	42.5	32.5
29	33.7	63.1	42.7	21.7	41.7	22.5	42.5	NA	27.2	31.5	36.3
31	36.3	25.4	51.2	41.0	58.3	9.74	46.4	0.44	24.6	47.7	42.3

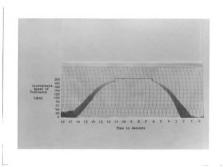
Cumulative Number of Beats of Post Rotatory Nystagmus; individual mean scores of individual mice. NA = Data not available - = Data not recorded

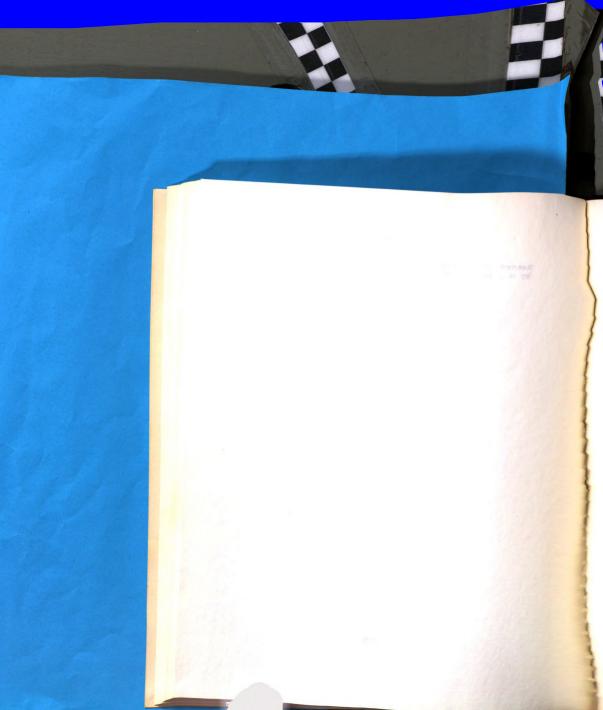




APPENDIX XII

Record of acceleration of the turntable. Curve was produced by a generator coupled directly to the turntable.







 $\label{eq:APPENDIX XIII} \mbox{Record of typical post rotatory nystagmus response.}$

