Development of the immobility response (animal hypnosis) in two species of deermice (*Peromyscus*)*

BEDFORD M. VESTAL†

Oklahoma City Zoo, Oklahoma City, Oklahoma 73111
and
University of Oklahoma, Norman, Oklahoma 73069

Immobility responses (animal hypnosis) to restraint were found in two species of deermice tested cross-sectionally at ages ranging from 11 to 22 days and as adults (60 days). Responses in *Peromyscus maniculatus* appeared at 13 days of age and, by 20 days, had increased to approximately adult levels of incidence. In *P. leucopus*, responses only occurred between 15 and 18 days and as adults. Response incidence is higher in juvenile *maniculatus* than in *leucopus*, while adults of the two species were not different. The developmental pattern of the response in *maniculatus* is similar to that in birds, but the *leucopus* pattern is different from others reported.

Immobility or animal hypnosis responses to manual restraint have been described in many species. The characteristic general response to restraint is struggling followed by a general state of immobility and unresponsiveness. It appears to be a fear response (review by Ratner, 1967). Support for the fear hypothesis has been found in chickens, lizards, and frogs by presenting animals with a noxious stimulus (shock or noise) prior to testing for immobility (Nash, Gallup, & McClure, 1970; Edson & Gallup, 1972; Gallup, Nash, Potter, & Donegan, 1970). Injection of adrenalin prior to testing also increases susceptibility to, and duration of, the response (Braud & Ginsburg, 1973a). The response has been interpreted as a form of death feigning, which may have evolved under selective pressure exerted by predation. Ratner (1967) hypothesized that responses to a predator may vary with the distance between the animal and the predator. At first detection, the animal may freeze and, with decreasing distance, flight and escape responses occur. As the distance decreases to zero, the animal may fight or, if restrained, may exhibit immobility. Since many predators continue to attack a prey animal only if it is moving, the immobility response may help avert further attack and injury and allow for escape during moments of inattention by a predator. Support for predators acting as fear stimuli, which affect immobility, has been found by Gallup, Nash, & Ellison (1971) in chickens. The immobility response appears to be different from the "freezing" response exhibited by many mammals. Foster (1959) noted that *Peromyscus maniculatus bairdi*

froze more often in open fields or threatening situations than did *P. m. gracilis*. According to Ratner's (1967) hypothesis, freezing is more of an alerting response, which occurs when the predator is some distance from the prey animal. Freezing could help avoid detection by reducing visual stimuli to the predator. Freezing responses in experimental situations typically do not last as long as immobility responses (Borchelt & Ratner, 1973), and freezing animals are highly responsive to external stimulation. In bobwhite quail, however, the duration of immobility may be reduced when external stimulation is provided (Doty, 1969).

The incidence (frequency) of immobility responses as well as the duration of the response in birds may change during development. Ratner and Thompson (1960) reported that, in chickens, immobility reactions induced by lateral inversion were low in both incidence and duration during the first week of life, but both increased rapidly during the second week and remained at a maximum until 59 days of age. Salzen (1963) corroborated the dramatic increase in immobility-response incidence in chickens during the second week through use of dorsal restraint. However, immobility responses have been elicited in chickens as early as 12 h posthatch (Rovee & Kleinman, 1974) by the use of ventral restraint at one day of age (Braud & Ginsburg, 1973b) through use of dorsal restraint in a cloth "trough." In the latter studies, response incidence was complete or high from the beginning but other response parameters changed with age. Response duration and eye closure increased while vocalizations decreased (Rovee & Kleinman, 1974). Bobwhite quail under lateral restraint also exhibit an increase in incidence and duration of immobility with age, but the first strong occurrence is between 9 and 15 days of age (Borchelt & Ratner, 1973). On the basis of earlier literature, the increasing incidence of the response with age was hypothesized by Ratner and Thompson (1960)

*Supported by Grant 5 RO1 EY00447 to John King and Training Grant TO1 GM1751 to Michigan State University from NIH, and by the Biology Department, University of Missouri-St. Louis. John King and D. J. Zerbolio commented on an earlier version of the manuscript.

†Reprint requests should be sent to Bedford M. Vestal, Animal Research Center, Oklahoma City Zoo, Rt. 1, Box 478, Oklahoma City, Oklahoma 73111.

to be correlated with developmental change associated with becoming independent of the parents. This explanation in chicks appears negated by the presence of the response in 12-h-old chicks (Rovee & Kleinman, 1974). Salzen (1963) attributed the increase to an increase in fear responses along with maturation of the neural mechanisms releasing the response. However, fear responses appear early in life, as does the immobility response (Braud & Ginsburg, 1973b). The maturation of neural controls has not been adequately explored, and no clear-cut explanation for response maturation has been developed.

Reports of development of immobility responses in mammals have indicated a different developmental pattern than in birds. On the basis of incompletely reported studies, Svorad (1957) asserts that susceptibility to animal hypnosis decreases in rats over the period from 1 to 15 days of age. The data were presented only in terms of duration (whether total or average, not shown) and not incidence. The decrease in response was attributed to development of the neocortex. This reasoning was supported by data from a phylogenetic series of adult animals with increasing development of the neocortex which showed that lizards and chickens were very susceptible, that rabbits were less so, and that rats and cats did not exhibit the response (data reported only as average duration). Better evidence for a mammalian developmental pattern is provided by McGraw and Klemm (1969). Rats under 10 days of age were very susceptible, and duration of response decreased with increasing age to a stable level at 20 days. This age corresponds with the maturation of the neocortex. The response was also induced in decorticate rats which were previously not susceptible, indicating the possible role of the neocortex in inhibiting immobility responses.

In the course of a developmental study of visual acuity in two species of *Peromyscus*, immobility responses commonly interfered with carrying out the experiments. Immobility responses have not been reported in mice. In this study, developmental changes in incidence of the response as well as species difference in incidence were recorded and compared to adult response frequency. If the response is a fundamental and basic reaction to restraint as proposed by Ratner (1967), the response should be prevalent in major prey species such as mice.

METHOD

Peromyscus maniculatus bairdi, the prairie deer mouse, and *P. leucopus noveboracensis*, the white-footed mouse, were the experimental Ss. *P. maniculatus* inhabits midwestern grasslands of the U.S. It is terrestrial in its habits (Howard, 1949) and behavior (Horner, 1954) and is smaller than *leucopus* (Burt, 1957). *P. leucopus* primarily inhabits upland hardwood forests and is semiarboreal in its habits (Nicholson, 1941; McCarley, 1963) and behavior (Horner, 1954). The two species exhibit similar developmental patterns in several morphological parameters (Layne, 1968; Vestal, 1973) in contrast to differences in adult ecology and behavior.

All mice used in the developmental part of this study were born and raised in the animal-behavior colony at Michigan State University. They were first- to fourth-generation descendants of animals wild-trapped in the vicinity of East Lansing, Michigan. One-hundred and ninety-six *P. leucopus* (99 males and 97 females) and 251 *P. maniculatus* (122 males and 129 females) were tested. With four exceptions, results are from single tests for each mouse. The four exceptions are *P. leucopus* which exhibited immobility during a second test. Results of both tests for these four mice are included.

Mice from litters of three to five young were used. From 10 days of age, litters were checked daily for eyelid separation. Animals were tested for visual acuity on the day of eye opening (Day 0) and Days 1, 2, 3, 4, 5, 6, and 8 after eye opening. This was without regard to the chronological age in days at the time of eye opening.

At the time of testing, animals were removed from the home cage, weighed, and restrained on a 12.5 x 10.9 cm platform by taping the tail to a flat piece of lead. Lateral and vertical movements were 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 platform was placed on a nonmoving central shaft in an optokinetic device (Vestal, 1973). The apparatus consisted of a rotatable wooden disk upon which upright 51-cm cylinders of 20- or 40-cm radii could be interchangeably mounted. Illumination was provided by an incandescent lamp in a metal reflector, covered with sheets of white paper to diffuse the light. Most tests were run at 86.1 lx light intensity with some at 4.3 lx and 861.1 lx (as measured at the S's position). The cylinders were lined with interchangeable striped panels. The vertical black and white stripes were of equal width, and stripes of various widths were used to determine visual acuity. The S platform was 30.5 cm above the floor in the 20-cm radius cylinder and 20 cm above the floor in the 40-cm cylinder.

After being restrained in the apparatus for 1 to 2 min, visual acuity testing began with large black and white stripes. If the Ss responded, further tests were run to determine visual acuity. In many cases animals, for some reason, did not respond. Some kept their eyes closed, struggled so violently that they could not be tested, or exhibited the immobility response while restrained in the apparatus. The immobility response was defined as one primarily of prolonged tonic immobility (Ratner, 1967). In the immobility response of deermice, the eyes were open and the animal maintained a given position until moved by E. Limbs could be flexed or extended and would remain in the new position. Loud noises, finger snapping, light flashes, movement of the optokinetic device, shock, poking, etc., generally did not bring the animal out of its state. In one case, a mouse was subjected to the above treatments and carried about in E's hand for 40 min while immobile. Upon being dropped into its home cage, the animal immediately resumed activity.

Immobility tests of a different type were also done with adult mice for comparison with the juveniles. Adults were 70 to 120 days of age and were born and raised in the colony of the University of Missouri, St. Louis. They were descended from (one to three generations removed) the Michigan State stock. Forty mice (20 males and 20 females) of each species were tested by grasping them firmly by the scruff of the neck and inverting them for 15 sec. An animal was scored as exhibiting immobility if it ceased moving (including sniffing movements of the nose) and became flaccid in posture. A hind leg could be either flexed or extended and would remain where placed. These characteristics correspond to descriptions of the response in other animals.

Immobility responses in deermice appear to differ in one important respect from those of birds. The response (in adults) ended almost immediately after restraint was removed. In several cases, I attempted lateral restraint of adults, but the animals jumped away as soon as I released the scruff of the neck. Juveniles sometimes remained immobile after restraint was

Table 1
Incidence of Immobility Response by Age in Days After Eye Opening at Time of Testing

Days After Eye Opening	<i>Peromyscus maniculatus</i>			<i>Peromyscus leucopus</i>		
	Number Tested	Number Immobile	Percent Immobile	Number Tested	Number Immobile	Percent Immobile
0	50	2	4.0	41	0	0
1	32	1	3.1	37	1	2.7
2	35	0	0	27	0	0
3	54	4	7.4	49	9	18.4
4	17	2	11.8	12	0	0
5	15	5	33.3	13	3	23.1
6	24	9	37.5	9	0	0
8	24	16	66.7	8	0	0
Total	251	39	15.5	196	13	6.6

removed, but while still in a strange situation such as on the test platform or in the E's hand. No durations were recorded but were in the range of less than 10 sec, as reported for rats by McGraw and Klemm (1969). When placed back in the home cage, the immobile Ss immediately became active.

Results were analyzed by means of χ^2 corrected for continuity and Fisher's exact probability test (Siegel, 1956).

RESULTS

The percentages of juvenile mice exhibiting responses are shown in terms of days after eye opening (Table 1) and age in days at the time of testing (Table 2). The *P. maniculatus* exhibited a developmental increase in frequency, while the *leucopus* only exhibited the response during a relatively short period. The total frequency of the response is higher in juvenile *maniculatus* than in *leucopus* ($\chi^2 = 7.65$, $df = 1$, $p < .01$). There was no sex difference in occurrence of the response in either species, in either juveniles or adults.

Test conditions varied greatly among the juveniles because the experiment was designed to study visual-acuity development. For example, high- and low-light intensities were used for mice at 3 days

post-eye-opening. Only one of 32 (3%) *P. M. bairdi* in the high- and low-light groups exhibited immobility. However, among *P. leucopus* 2 of 11 (15%) of the high-light group and 6 of 16 (27%) of the low-light group became immobile. These two groups together account for 8 of the 13 (69%) immobile *P. leucopus*. In view of the small numbers involved, it is difficult to explain this difference in response of the *P. leucopus*. Because of the small total numbers of responders, the juvenile data were left combined for comparison with the adults.

For the adults, results from both sexes were combined. In *P. leucopus*, 21 of 40 exhibited immobility while in *P. m. bairdi*, 28 of 40 did so. The difference is not significant ($\chi^2 = 1.90$, $df = 1$).

Incidence of the immobility response is significantly higher in adult *P. leucopus* than in juveniles (Table 2, juveniles of all ages combined, $\chi^2 = 53.0$, $df = 1$, $p < .001$). In *P. m. bairdi*, the adult incidence is higher than in juveniles when the data from all juveniles are combined ($\chi^2 = 54.7$, $df = 1$, $p < .001$). However, by age 18 days, one-third of the juvenile *bairdi* exhibited the response (Table 2). When incidence at age 19 days is compared to the adults, it is significantly lower ($p = .006$, Fisher's exact probability), but the incidence

Table 2
Incidence of Immobility Response by Age in Days at Time of Testing

Days of Age	<i>Peromyscus maniculatus</i>			<i>Peromyscus leucopus</i>		
	Number Tested	Number Immobile	Percent Immobile	Number Tested	Number Immobile	Percent Immobile
11	2	0	0	1	0	0
12	17	0	0	21	0	0
13	34	2	5.9	31	0	0
14	40	1	2.5	39	0	0
15	36	2	5.6	34	6	17.6
16	36	2	5.6	28	3	10.7
17	30	6	20.0	19	1	5.3
18	15	5	33.3	7	3	42.9
19	10	4	40.0	8	0	0
20	15	7	46.7	3	0	0
21	13	7	63.6	4	0	0
22	5	3	60.0	1	0	0
Total Juveniles	251	39	15.5	196	13	6.6
Adults (70-120)	40	28	70.0	40	21	52.5

in juveniles 20 days of age is not different from the adults ($p = .07$, Fisher's exact probability). These data indicate that juvenile *P. m. bairdi* reach the adult level of response by 19 to 20 days of age. The development of the response in *P. leucopus* evidently takes longer, and the peak is reached in the postjuvenile period.

DISCUSSION

The immobility response is different from freezing behavior. Any investigator who has recaptured an escaped deermouse by hand will recognize that animals will often freeze in response to loud noises. As an attempt is made to close the distance for capture, the mouse begins running and, if grasped, will begin struggling and will attempt to bite. Only after firmly holding the mouse does the immobility response occur. Freezing thus appears to be a means of reducing probability of detection by predators, but the animal is still alert and ready to flee if the predator approaches. Immobility responses occur at the last stage of capture and may reduce the possibility of injury and, perhaps, produce an opportunity for escape from a predator.

Incidence of the response increased rapidly with age in *P. maniculatus*, especially from Days 4-8 after eye opening and Days 16-22 of age. By 19 to 20 days of age, the response incidence had essentially reached the adult level. In *P. leucopus*, the response only occurred between Days 3 and 5 after eye opening and Days 15-18 of age. Incidence of the response in juveniles was much lower than in adults. The continuing increase in incidence in *bairdi* is much like the pattern observed in chickens (Ratner & Thompson, 1960) and bobwhite quail (Borchelt & Ratner, 1973). Later authors found that chickens would exhibit the response very early and had no increase in incidence, but other parameters of the response did show a pattern of developmental change (Rovee & Kleinman, 1974). In birds, Ratner and Thompson (1960) hypothesized that increasing incidence of immobility is correlated with development of physical independence. In both deermouse species, the period when the response begins to occur is one of rapid development. For example, visual acuity is rapidly improving (Vestal, 1973), and other physical and behavioral processes are maturing (Layne, 1968). The period from Days 13-17 of age (mean of 15) is also the age at which young mice of both species will begin voluntarily to leave their nests and to explore the vicinity (Vestal and Coleman, unpublished data). This simultaneous development of independence and immobility incidence leads to further questions. What is the function of the response in older animals that is not found in younger ones? What is the significance of the species difference in developmental pattern in view of the similar frequencies of response in the adults? What explains the difference in developmental patterns between deermice and rats, with rats being all

susceptible prior to 15 days of age, followed by decreasing susceptibility (McGraw & Klemm, 1969)?

If the predator-response hypothesis of Ratner (1967) is correct, then there should be selection for an increasing incidence of this response with age. Presumably, mice which venture out of the nest will be more exposed to predation than young still in the nest. This exposure could have led to selection for development of the response.

The question of species differences is more difficult to determine. In *P. maniculatus*, the pattern of increase corresponds to that seen in various bird species which reach a high level of response as they become independent of the parents. *P. leucopus* juveniles only exhibit the response for a short period of time. In this species, the response has the same developmental pattern as the "jumpy" phase in some strains of mice in which, for a short period, the mice are very sensitive to external stimuli. The jumpy phase in *P. m. bairdi* peaks at about 15 days of age (King, 1958) but has not been described in *P. leucopus*. If the immobility response has selective value and is prevalent in adult *leucopus*, why does it have such a low incidence of occurrence over such a short time span in the juveniles, as compared to juvenile *maniculatus*? One might hypothesize that, if the response is a predator defense mechanism, the terrestrial *P. m. bairdi* might be exposed to predation at an earlier age. The semiarboreal *P. leucopus* might not have been selected for early development of the response because of a lower incidence of predation at early ages. However, *P. leucopus* spends a great deal of time on the ground and therefore would also be exposed to predators as soon as it is independent. Another possibility might be the development of a competing response or a higher threshold for release of the immobility response.

The developmental patterns of *P. m. bairdi* and *P. leucopus* differ less from each other than they differ from that of rats. Svorad's (1957) rats declined in susceptibility from high at 1 day of age to being unsusceptible after 15 days. McGraw and Klemm (1969) report 100% incidence of the response before 15 days; it declined to 50% at 4 months and to 37.5% at 10 months. McGraw and Klemm describe the adult percentages of susceptibility as "low." However, they are not significantly different from the adult deermice at 61% incidence (4 months, $\chi^2 = 1.24$, $df = 1$; 10 months, $\chi^2 = 2.1796$, $df = 1$, $p > .10$). Rats and deermice have similar levels of susceptibility among adults, but they reach these levels from different directions. Susceptibility in both groups is lower than that reported for birds by numerous authors.

Phylogenetic differences in susceptibility between birds, reptiles, and mammals was explained by Svorad (1957) as an example of greater neocortical development in mammals, with the neocortex inhibiting the immobility response. This view of neocortical inhibition was supported by McGraw and Klemm (1969) with their

developmental and decortification studies in the rat. The extent of neocortical development in *Peromyscus* is still unclear (Klingener, 1968), so we cannot say how brain structure may affect the pattern of responses.

The gross differences in developmental pattern between the two *Peromyscus* species is still not explained; neither is the even greater developmental difference between deermice and rats. The problems posed by these differences indicate the need for further studies, including a comparison of the response in several semiarboreal and terrestrial species of *Peromyscus* to determine ecological correlations. A more complete developmental study of the response, along with its physiological and developmental correlates is also indicated. The developmental work should include several genera of rodents to help elucidate the phylogenetic pattern and ecological correlates of the response.

REFERENCES

- Borchelt, P. L., & Ratner, S. C. Development of freezing and immobility, predator defenses, in the bobwhite quail (*Colinus virginianus*). *Behavioral Biology*, 1973, 8, 83-92.
- Braud, W. G., & Ginsberg, H. J. Effect of administration of adrenalin on immobility reaction in domestic fowl. *Journal of Comparative & Physiological Psychology*, 1973a, 83, 124-127.
- Braud, W. G., & Ginsburg, H. J. Immobility reactions in domestic fowl (*Gallus gallus*) less than 7 days old: Resolution of a paradox. *Animal Behavior*, 1973b, 21, 104-108.
- Burt, W. H. *Mammals of the Great Lakes Region*. Ann Arbor: University of Michigan Press, 1957.
- Doty, R. L. The effect of environmental movement upon the duration of tonic immobility in bobwhite quail. *Psychonomic Science*, 1969, 16, 48-49.
- Edson, P. H., & Gallup, G. G., Jr. Tonic immobility as a fear response in lizards (*Anolis carolinensis*). *Psychonomic Science*, 1972, 26, 27-28.
- Foster, D. D. Differences in behavior and temperament between two races of the deermouse. *Journal of Mammalogy*, 1959, 40, 496-513.
- Gallup, G. G., Jr., Nash, R. F., Potter, R. J., & Donegan, N. H. Effect of varying conditions of fear on immobility reactions in domestic chickens (*Gallus gallus*). *Journal of Comparative & Physiological Psychology*, 1970, 73, 442-445.
- Gallup, G. G., Jr., Nash, R. F., & Ellsion, A. E., Jr. Tonic immobility as a reaction to predation: Artificial eyes as a fear stimulus for chickens. *Psychonomic Science*, 1971, 23, 79-80.
- Horner, B. E. Arboreal adaptations of *Peromyscus* with special reference to the tail. Contributions of the Laboratory of Vertebrate Biology, University of Michigan, 1954, 61, 1-84.
- Howard, W. E. Dispersal, amount of inbreeding, and longevity in a local population of deermice on the George Reserve, Southern Michigan. Contributions of the Laboratory of Vertebrate Biology, University of Michigan, 1949, 43, 1-52.
- King, J. A. Maternal behavior and behavioral development in two subspecies of *Peromyscus maniculatus*. *Journal of Mammalogy*, 1958, 39, 177-190.
- Klingener, D. Anatomy. In J. A. King (Ed.), *Biology of Peromyscus (Rodentia)*. American Society of Mammalogists, Special Publication No. 2, 1968. Pp. 127-147.
- Layne, J. N. Ontogeny. In J. A. King (Ed.), *Biology of Peromyscus (Rodentia)*. American Society of Mammalogists, Special Publication No. 2, 1968. Pp. 148-253.
- McCarley, W. H. Distributional relationships of sympatric populations of *Peromyscus leucopus* and *P. gossypinus*. *Ecology*, 1963, 44, 784-788.
- McGraw, C. P., & W. R. Klemm. Mechanisms of the immobility reflex ("Animal Hypnosis") III. Neocortical inhibition in rats. *Communications in Behavioral Biology*, 1969, Part A, 3, 53-59.
- Nash, R. F., Gallup, G. G., Jr., & McClure, M. K. The immobility reaction in leopard frogs (*Rana pipiens*) as a function of noise-induced fear. *Psychonomic Science*, 1970, 21, 155-156.
- Nicholson, A. J. The homes and social habits of the woodmouse (*Peromyscus leucopus noveboracensis*) in southern Michigan. *American Midland Naturalist*, 1941, 25, 196-223.
- Ratner, S. C. Comparative aspects of hypnosis. In J. E. Gordon (Ed.), *Handbook of clinical and experimental hypnosis*. New York: MacMillan, 1967. Pp. 550-587.
- Ratner, S. C., & Thompson, R. W. Immobility reactions (fear) of domestic fowl as a function of age and prior experience. *Animal Behavior*, 1960, 8, 186-191.
- Rovee, C. K., & Kleinman, J. M. Developmental changes in tonic immobility in young chicks (*Gallus gallus*). *Developmental Psychobiology*, 1974, 7, 71-77.
- Salzen, E. A. Imprinting and the immobility reactions of domestic fowl. *Animal Behavior*, 1963, 11, 66-71.
- Siegel, S. *Nonparametric statistics*. New York: McGraw-Hill, 1956.
- Svorad, D. "Animal Hypnosis" (Totstellreflex) as experimental model for psychiatry. *AMA Archives of Neurology & Psychiatry*, 1957, 77, 533-539.
- Vestal, B. M. Ontogeny of visual acuity in two species of deermice (*Peromyscus*). *Animal Behavior*, 1973, 21, 711-719.

(Received for publication November 7, 1973;
revision accepted July 9, 1974.)