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Circadian rhythms of tonic immobility in the rat: Evidence of an endogenous mechanism

CHARLES W. HENNIG and WILLIAM P. DUNLAP
Tulane University, New Orleans, Louisiana 70118

Circadian rhythms of tonic immobility were found in male albino rats raised on a 12-h diurnal light cycle and tested at 6-h intervals. Durations of immobility were twice as long at 2000 h as at 1400 h. These differences persisted when rats were exposed to constant darkness for 10 days, but disappeared when rats were maintained in constant light for the same period. Since endogenous circadian rhythms of certain monoamine levels persist in constant darkness yet disappear under constant light, it is suggested that cycles of tonic immobility in rats are also endogenous. When the diurnal pattern of tonic immobility duration is compared to that of various neurohumors, immobility duration appears to parallel melatonin production and to be opposite in phase to the cycle of serotonin levels. Duration of immobility increased over trials, although the number of inductions required to produce immobility decreased. This suggests that instrumental conditioning may modify the immobility response to some extent.

Many behaviors, in a number of species, run in cycles or rhythms that vary in length. Most animals show circadian rhythms in their patterns of feeding and drinking, vocalization, and gross motor activity (Marler & Hamilton, 1966). Presumably, evolution has selected circadian rhythms in common behaviors that approximate the important cycles in the physical environment, thus allowing maximum efficiency of time and resources (Halberg, 1960). Although the precise mechanisms underlying circadian rhythms have not yet been identified, a number of hypotheses exist that attempt to explain these phenomena. The two most common explanations are the endogenous and exogenous hypotheses (for a review, see Brown, Hastings, & Palmer, 1970). Proponents of the exogenous hypothesis maintain that circadian cycles result from intracellular rhythms entrained to geophysical fluctuations (Wallace, 1973); common entraining agents are thought to be light-dark cycle, day length, and temperature (Aschoff, 1962). The endogenous hypothesis maintains that these rhythms are under control of an innate biochemical "clock" that may be influenced by environmental changes but is not entirely dependent upon them (Wallace, 1973).

Tonic immobility (TI), also commonly referred to as animal hypnosis, is a behavior that has recently received much experimental attention. This response, observed in a variety of species, is produced by manual restraint and characterized by a prolonged state resembling paralysis. The immobility response appears to represent an innate fear reaction (Gallup, 1974; Gallup, Nash, Donegan, & McClure, 1971; Gallup, Rosen, & Brown, 1972), and a number of studies have demonstrated its involvement in simulated and actual predatory encounters (Gallup, 1973; Gallup, Nash, & Ellison, 1971; Sargeant & Eberhardt, 1975). In the context of a predatory theory of TI, one might except cyclic changes in the susceptibility of this behavior as a function of time of day, depending on such factors as when an animal is most active and consequently more subject to predation.

Recently, several studies have examined the circadian rhythms of tonic immobility in a variety of species. Ternes (1977) has reported that duration of TI varied with time of day for testing in both a species of toad (*Bufo marinus*) and a species of tarantula (*Cyrtopholis potoricae*), with the toads showing longest durations of TI around dawn and the tarantulas showing longest durations around midnight. Both species are nocturnal. Hennig and Dunlap (in press) have found longer durations of TI at night than during the day in two species of lizard (*Hemidactylus turcicus* and *Anolis carolinensis*), although the former is a nocturnal animal while the latter is diurnal. Piroch (1974) has examined circadian rhythms of immobility in young domestic chickens and found longer durations of TI at night than during the day in that species also.

Similarities in the rhythmic cycles of tonic immobility in these diverse species, comprising both nocturnal and diurnal animals, suggest that some explanation other than general activity cycles are involved in these daily changes, perhaps of some as yet unknown biochemical nature. The existence of such cycles of TI in another nocturnal animal, the albino rat, was explored in the present study and the

Requests for reprints should be sent to Charles W. Hennig, Department of Psychology, Tulane University, New Orleans, Louisiana 70118.

question of whether such cycles are endogenous or exogenous was examined. Since the biochemical cycles of the rat have been studied extensively, research using this species may also permit comparisons of cycles of TI with those of neurotransmitters whose involvement in the mediation of TI is suspected. The albino rat has been regarded as a poor subject for studies of TI (McGraw & Klemm, 1969, 1973; Ratner, 1967; Svorad, 1957; Teschke, Master, & Gallup, 1975); the present study documents methodology by which TI can be elicited reliably in rats and quantifies some behaviors of the rat during immobility episodes.

EXPERIMENT 1

The first experiment was designed to determine if there are cyclic rhythms for either duration of tonic immobility or the number of inductions required to produce TI, and to delineate other aspects of immobility behavior.

Method

Subjects. Twenty-four experimentally naive male albino rats of the Charles River strain, 85-90 days of age at the time of testing, were used as subjects. The rats were housed two to a cage until they reached 60 days of age, at which time they were moved to individual cages. Purina Rat Chow and water were available ad lib. A light/dark cycle, in which the light was provided by four sets of fluorescent ceiling fixtures and the dark by their absence, with the lights off between 1800 h and 0600 h, was in effect throughout the study.

Apparatus. A large cardboard box was used to transport each rat individually to the sound-attenuated testing room, which was lighted by a single 15-W bulb in a lamp with a frosted glass cover. The animals were immobilized in a wooden trough, 30 cm long and 16 cm wide at the top, which sloped from 8 cm at the sides to 2 cm at the middle, and which prevented subjects from accidentally rolling on their sides and terminating immobility episodes prematurely. A stopwatch was used to time durations of immobility, and leather gloves were used to handle all animals.

Procedure. At the start of testing, the subjects were divided into four equal groups of six rats each. The first group was tested for tonic immobility at 0800 h, the second group at 1400 h, the third at 2000 h, and the fourth at 0200 h. After a 1-day interval, each group was tested at another of the four times of day. This procedure was repeated four times, with a 1-day interval between each test period, such that each rat was tested at all four times of day. The individual sequence of testing for tonic immobility was as follows. The subject was taken from its cage and carried in a closed cardboard box to the dimly lit testing room. The experimenter seized the rat in the cervical area with his right hand and quickly inverted it on its back in the wooden trough. Pressure was maintained on the body of the rat with the experimenter's left hand, while the rat's head was held firmly in place by his right hand on the subject's lower jaw; however, care was taken to avoid occlusion of neck vessels and trachea. Restraint was gradually reduced by removal of the experimenter's left hand from the rat's body, so that its head was the only part held rigid. If the animal began struggling again at this time, the experimenter replaced his hand on the rat's body until struggling ceased once more. Restraint was maintained until immobility was evident, or until 30 sec had elapsed. Ratner (1967) reported 30 sec to be the optimal induction time for TI in rats. A stopwatch was activated when TI was obtained and deactivated when the rat started to right itself. If the subject did not remain immobile for at least 4 sec (the criterion set by McGraw & Klemm, 1969), restraint was immediately reapplied for another 30-sec period. The restraint procedure was repeated for a maximum of 20 inductions. If the subject did not go immobile within these 20 attempts, it was considered not susceptible and received a duration score of 0 sec. Following testing, each subject was returned to its home cage and both the duration of TI and the number of inductions were recorded.

Results

Although rats show less susceptibility to TI and relatively short durations of immobility when compared to chickens or lizards (Gallup, 1974), they still show many of the characteristics typical of the immobility response seen in other species. After a brief struggle, the rats showed extreme rigidity, often accompanied by tremor, changes in respiration rate, and a lack of responsiveness to normal stimuli. Moreover, there was one behavior shown by rats toward the termination of the immobility episodes which has not been noted in other species; they were seen to sniff the air immediately prior to termination of the response on many of the trials.

The mean durations of tonic immobility and standard errors of the mean for the four test periods at 6-h intervals are shown in Figure 1. As can be seen in this figure, there was a clear increase in the duration of TI from 1400 to 2000 h. An analysis of variance for the Latin-square design (Winer, 1971) revealed a significant difference in durations of TI over the four times of day for testing, $F(3,60) = 3.12$, $p < .05$. Subsequent Newman-Keuls tests revealed that only the duration of TI at 2000 h differed significantly ($p < .05$) from that at 1400 h. The mean durations of tonic immobility over Days 1 to 4 of testing were 7.6, 15.2, 16.3, and 20.6 sec, respectively, demonstrating an increase in the length of dura-

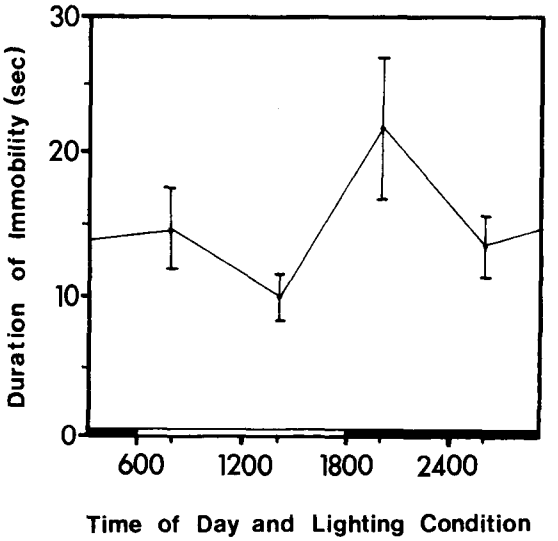

Figure 1. Mean durations of tonic immobility and standard errors of the mean as a function of time of day.

tions with repeated testing. Analysis of these data showed days to be a significant factor, $F(3,60) = 3.92$, $p < .025$, with subsequent Newman-Keuls comparisons indicating that only the duration on the first day of testing was significantly different ($p < .01$) from that on the last day. There were no significant effects due to either order of testing or the Order by Time of Day interaction. Number of inductions required to produce TI did not appear to vary as a function of time of day (see Table 1). However, the mean number of inductions over Days 1 to 4 were 16.5, 11.8, 7.9, and 7.7, respectively, demonstrating that TI was significantly easier to induce after repeated testing, $F(3,60) = 17.19$, $p < .001$. Newman-Keuls comparisons of these data showed that the mean number of inductions on the first day of testing differed significantly ($p < .01$) from those on the other days and that the number of inductions on the second day differed significantly ($p < .05$) from those on the last 2 days. There were no significant differences in the number of inductions due to either order or the Order by Times interaction.

EXPERIMENT 2

The finding, in Experiment 1, of a temporal cyclicity for immobility durations in the rat raises the important question of whether this cycling is endogenous, as many rhythms seem to be, or if the cycling is simply tied to exogenous factors. To be classified as endogenous, circadian cycles must meet certain logical requirements, such as persistence in the absence of a fluctuating photoperiod. The second experiment was designed to determine whether the difference in duration of TI between 1400 and 2000 h, found in Experiment 1, persists in constant darkness.

Table 1
Means and Standard Deviations for Durations of Tonic Immobility and the Number of Inductions Required to Produce TI at Different Times of Day in Normal Light Conditions, Constant Dark, or Constant Light

Time of Day†	n	Duration of Immobility (sec) M	Duration of Immobility (sec) SD	Number of Inductions M	Number of Inductions SD
Experiment 1: Normal Lighting					
0800	24	14.7	15.6	11.8	8.0
1400	24	10.1	8.1	9.8	6.2
2000	24	21.5	24.6	11.6	7.1
0200	24	13.5	11.0	10.7	6.6
Experiment 2: Constant Dark					
1400	10	8.1	3.0	4.6	2.5
2000	10	19.4	15.7	7.6	6.3
Experiment 3: Constant Light					
1400	20	19.4	28.7	6.9	6.1
2000	20	22.6	29.2	4.1	2.7

**Subjects were tested in a Latin square repeated measures design.* *†Clock hour*

Method

The subjects were 10 experimentally naive male albino rats of the Charles River strain, 85-90 days of age at the time of testing, reared in the same manner as those in the first experiment, except that 10 days before testing they were switched from the normal light cycle to constant darkness. Using the same apparatus as in the previous experiment, these animals were tested for tonic immobility. They were separated into two groups of five each, with one group tested at 1400 h and the other at 2000 h. Then they were given a day of rest and each group was tested at the other time of day, so that all subjects were tested at both times. The induction procedure and other details were the same as in the first experiment.

Results

Longer durations of TI at 2000 h as compared to those at 1400 h, as found in the first experiment, were also found in rats kept in constant dark for 10 days prior to testing. As shown in Table 1, the mean duration of TI at 2000 h was more than twice as large as that at 1400 h. Analysis of variance for the Latin-square design showed a significant difference due to time of testing, $F(1,8) = 7.15$, $p < .05$. The mean durations over days, 11.8 and 15.7 sec, indicated a similar trend to that in the previous experiment for longer durations after repeated testing, but neither these differences nor those due to order of testing approached significance. The mean number of inductions are also shown for both times of day in Table 1. Although immobility was harder to induce at night, the differences did not approach significance. The number of inductions over Days 1 and 2 (7.2 and 5.0, respectively) showed a trend toward greater susceptibility to TI with more exposure to induction, but neither these nor those differences due to order of testing reached significance.

EXPERIMENT 3

The second experiment demonstrated that cyclicity for immobility durations occurs during constant darkness in rats in the absence of a fluctuating photoperiod; this lends support to the endogenous nature of this rhythm. The third experiment was designed to determine if the cycle in tonic immobility also persists in constant light, as it did under constant dark in Experiment 2. It is not necessary for the cycling to persist under both constant dark and constant light for an endogenous theory of circadian rhythms to be maintained, since one of these conditions, e.g., constant light, may trigger a constant high level of the behavior and override the underlying cyclicity. This lack of cyclicity in constant light is known to occur for a number of biochemical circadian rhythms in the rat (Klein, 1974; Klein & Weller, 1970; Ralph, Mull, Lynch, & Hedlund, 1971; Reiter & Klein, 1971; Snyder, Zweig, Axelrod, & Fischer, 1965), and the present experiment attempts to determine if the cycle of TI follows a similar course.

Method

The subjects were 20 experimentally naive male albino rats reared in the same manner as those in the first experiment, except that 10 days before testing they were switched from the normal light cycle to one of constant light. The subjects were divided into two groups of 10 each and tested for tonic immobility at the same times and in the same manner as in the second experiment.

Results

The means and standard deviations for both duration of TI and number of inductions required to produce TI at both 1400 and 2000 h are shown in Table 1. There was little difference for either measure as a function of time of day, and analysis of variance failed to show these factors to be significant. The durations of TI from Day 1 to Day 2 (14.1 and 27.9 sec, respectively) showed a significant difference, $F(1,18) = 5.05$, $p < .05$, with longer durations on the second day of testing. The number of inductions required from Day 1 to Day 2 (7.4 and 3.7, respectively) showed that TI was significantly easier to induce after repeated testing, $F(1,18) = 7.03$, $p < .025$. There was no significant difference due to order of testing for either of these dependent variables.

DISCUSSION

Although several studies have examined tonic immobility in the rat (McGraw & Klemm, 1969, 1973; Svorad, 1957; Teschke, Maser, & Gallup, 1975), most of this work has dealt with the relative nonsusceptibility of this species to TI and little has been done to examine the methods used to induce TI in the rat or the characteristics of the response. In previous studies, rats were usually restrained on a flat surface, which permits the subject to roll over and prematurely terminate the immobility episode; in the present study, rats were immobilized in a wooden trough to help prevent rolling. In addition, each subject's head was held rigidly in place, a procedure found to help maximize the immobility response in squirrel monkeys (Hennig, 1976). Since many predators seize their prey in the region of the head, this induction procedure may better simulate natural predatory episodes. Furthermore, holding the head rigid prevents the defensive reaction of biting, a reaction which might compete with tonic immobility.

Another difference in procedure in the present study is that only the first immobility episode score was recorded in any test session, while previous studies used an average of several duration scores. Compared to previous research using rats, the present study found considerably greater susceptibility to TI as well as noticeably longer mean durations. Although some rats failed to show TI on the first day of testing, all subjects showed it by the third day. The median number of inductions required to produce TI was 11, while the range for durations of TI was from 0 to 120 sec. Several subjects showed a strong immobility response on the first induction attempt, suggesting that TI is not simply an instrumentally conditioned response that the rat learns in order to avoid further seizure and restraint.

The physical characteristics of the immobility response in rats were similar to those of other species (see Ratner, 1967, for a review). After a brief struggle against the experimenter, the rat assumed a frozen posture, during which tremor was often seen in the extremities, there was occasional defecation, a lack of vocalization, and changes in the respiration rate. However, there were two differences from what is seen during TI in most other species. Many of the rats showed a sniffing response shortly before termination of the immobility episode. Anoles and chickens often show head movements that suggest a visual examination of the immediate environment before termination of TI episodes, and the albino rat, which relies heavily on its sense of smell, appears to show a comparable behavior employing another sensory system. The second difference seen in rats was that they required many more inductions to produce TI than either chickens (Gallup, Nash, & Wagner, 1971) or anoles (Edson & Gallup, 1972); also, the rats showed much more fighting, biting, and scratching than these other species. This seems to suggest that although tonic immobility may have developed in the rat as a predator defense, it is not now a predominant response and occurs only after a number of other defenses have failed. Since the rat has a variety of active predator defenses, response competition may account for the relatively poor susceptibility of the rat to TI when compared to other more defenseless species.

All three experiments in this study showed an increase in duration of TI over days, while there was a corresponding decrease in the number of inductions. Although chickens are known to habituate rapidly to TI over trials (Gallup, Nash, & Wagner, 1971), an increase in duration of immobility is not unknown. Bayard (1957) and Liberson (1948) reported increases in durations of TI in guinea pigs under conditions of massed practice. Nash and Gallup (1976) also found a similar result with chickens. Since restraint was immediately reapplied in the present study, if a subject did not go immobile, then, to the extent that successive inductions are aversive, repeated testing for TI at short intertrial intervals in this study may have, in effect, punished the subject for showing a righting response and caused the rats to remain instrumentally immobile for prolonged periods as a means of avoiding further restraint, as suggested by Nash and Gallup (1976).

The first experiment showed that a circadian rhythm for duration of tonic immobility exists in the

rat. These daily changes are most dramatic around the change from bright to dim illumination, with a mean duration of TI at 2000 h that was double that found at 1400 h; durations at the other times of testing did not appear to differ significantly. The second experiment showed that the circadian changes in duration of TI persisted after 10 days exposure to constant darkness, with little or no appreciable drift, while the third experiment showed that circadian cycles of TI disappeared if the subjects were kept in constant light. These findings with TI closely parallel findings with circadian cycles of several indole metabolites in the rat, which are thought to be endogenous. These biochemical cycles also appear to persist in constant darkness but disappear under conditions of constant high illumination (Klein, 1974). Therefore, the present results lend support to the belief that circadian rhythms of TI in rats are endogenous. Clearly, this interpretation is a tentative one, since one might argue that lighting is not the only, or even most salient, exogenous factor to examine. In the absence of a cycling photoperiod, behavior may become entrained to other less obvious diurnal or nocturnal changes, such as background noise, temperature, feeding, and cage cleaning periods, etc. Another important factor limiting the conclusiveness of the present findings is drift of circadian rhythms under constant conditions. Aschoff's rule (see Marler & Hamilton, 1966) maintains that virtually all free-running rhythms drift and that the directions and degree of drift depend upon the illumination level; with faster than 24-h periodicity and greater drift usually accompanying constant high illumination. Therefore, if the times of the minimum and maximum durations for the immobility cycle shifted with 10 days of constant light, the time at which TI was investigated may no longer have been optimum. It is not possible, however, to monitor TI continuously around the clock; but it was found that the duration scores in Experiment 3 at both sampled times were in the range of the greatest scores seen in Experiments 1 or 2, suggesting that constant light possibly produces consistently high immobility scores, wiping out the underlying cycle. Such findings would not be inconsistent with the behavior of a number of biochemical rhythms in the rat pineal gland (for a review, see Klein, 1974), which persist in constant darkness but show no evidence of cycling under constant light, when tested at numerous intervals, and very little evidence of drift.

A number of previous studies have shown circadian rhythms for durations of tonic immobility in other species, with a predominance of longer durations at night than during the day. Ternes (1977) found this in tarantulas, Piroch (1974) in chickens, and Hennig and Dunlap (in press) in anoles and geckos, although two of these species are nocturnal, like the rat, while the other two are diurnal. However, Ternes found that longest durations of TI in toads to be around dawn, but his subjects were housed outdoors, which may have confounded lighting conditions with temperature and other factors, while the other researchers used controlled conditions of lighting and temperature. Therefore, although there is a great similarity in circadian cycles across a number of various diurnal and nocturnal species, there are still some exceptions yet to be explained. Among these differences are the fact that circadian cycles of TI durations in geckos and anoles persisted in constant light (Hennig and Dunlap, in press), while the differences in TI in rats disappeared under the same conditions. Another major difference between species is that Piroch (1974) found the largest change in TI in chickens was around the dark-to-light shift, while in rats it centers around the light-to-dark illumination change. Perhaps this difference is related to the daily activity cycles of the two species. This still leaves the question of what mechanism is responsible for the circadian rhythms of TI in the rat and the similarities across species.

One of the main reasons for examining circadian cycles of TI in such an intractable species as the rat is that so much data exists for this species concerning circadian cycles of neurohumors. A number of studies have implicated the participation of various neurochemicals, particularly serotonin and the serotonergic neurons, in the mediation of tonic immobility (Boren, & Gallup, 1976; Gallup, Wallnau, Boren, Gagliardi, Maser, & Edson, in press; Hoagland, 1928; Liberson, Bernsohn, Wilson, & Daly, 1964; Maser, Gallup, & Hicks, 1975). If these neurochemicals are indeed involved with the mechanism responsible for tonic immobility, then the daily changes in their concentration levels would be expected to correspond to the circadian cycle of TI in the present study. Serotonin levels in the rat pineal gland (Axelrod, 1974; Quay, 1963; Snyder, Zweig, Axelrod, & Fischer, 1965) and in the hypothalamus, frontal cortex, and brainstem (Quay, 1968) have cycles that are opposite in phase to the cycle of immobility duration in the present study. Pineal melatonin (Quay, 1964; Ralph, Mull, Lynch, & Hedlund, 1971), on the other hand, showed a circadian cycle that corresponds rather closely to the TI cycle in rats. As further support for this apparent relationship in a different species, Pang, Ralph, and Reilly (1974) show pineal melatonin cycles in chickens that are in the close agreement with cycles of TI durations reported by Piroch (1974) in that species. Since serotonin is a biochemical precursor of melatonin, the prior studies which found effects by serotonin manipulations on TI are not really contradictory to a possible endogenous melatonin-TI relationship.

These findings tend to suggest that it may be the conversion of serotonin to melatonin in the pineal gland that is responsible for the circadian cycles of TI in the rat and perhaps implicates melatonin in the control of immobility. Although these relations are purely correlative and across studies as opposed to within, they do provide a possible direction for future research aimed at uncovering physiological substrates of the immobility response.

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