Cardiac and Respiratory Function During Sudden Prolonged Immobility in Wild Rodents

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Recently captured wild rodents of six different species were tested in a standard "open field" arena where they were subjected to sudden visual and auditory stimulation as well as to a natural predator. Periods of prolonged immobility ranging from 2 to more than 60 minutes' duration were elicited in 21 members of four species. This behavioral state was accompanied by very low heart rates and a high incidence of cardiac arrhythmias. Nine members of two other species which did not show prolonged immobility, had increased heart rates during testing and a significantly lower incidence of arrhythmias. Respiratory rate was elevated during testing in all species. Physiologic recordings were also obtained during "feigned death" responses and transient "torpor." The adaptive value of these responses is discussed, and the physiologic changes compared to those known to occur during syncope, sleep, expectation of attack and sudden death.

Prolonged immobility in the face of overwhelming threat is a fundamental behavioral response which occurs throughout the phylogenetic range from insects to man. Yet, despite the curiosity of naturalists (1) and other investigators (2), there have been few studies of the adaptive value of such behavior under natural conditions and our knowledge of the physiology of this state is minimal (3, 4). The phenomenon of sudden prolonged immobility has been known to occur in animals since 1646 when Kircher (5) described a state of "entrancement" in hens induced by certain manipulations, which he attributed to the powers of the hen's imagination. A variety of names have been used since Wilson, in 1839 (6), listed it as a form of hypnosis. Darwin (7) coined the term "death-feint," while more recently, Hoagland (8) and others have used the term "tonic immobility." The eliciting situation has been widely variable among observers, but the elements of suddenness, environmental dislocation and physical constraint were common.

While participating in a previous study on the escape behavior of newly captured wild rodents (Rouger and Tobach, in preparation), I was very impressed by one or two examples of prolonged splay-legged immobility shown by chipmunks upon forced emergence into an unfamiliar setting, and I determined to discover more about the stimuli necessary to elicit this

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behavior, its incidence among other species, and some of the concomitant physiologic changes. As a part of a long-term investigation of the development of cardiac neural regulation, I had observed similar behavior in the laboratory when 16- and 20-day-old Wistar strain rat pups were subjected to a sudden noise in unfamiliar surroundings. Immobility lasted as long as 5 min and was associated with profound decreases in heart rate and increased respiratory rates (9).

The present study was designed to observe and make physiologic recordings from a number of different species of recently captured wild rodents suddenly exposed to an experimental testing arena ("open-field") and then subjected to the added stimulation of a "low-flying" artifical hawk-silhouette, a loud, high pitched noise and finally a natural predator, the snake. A polygraph record of heart rate, EKG-EMG and respiration was made throughout so as to give a profile of function for each animal. In addition, after several days' adaptation, basal levels were recorded while each animal was asleep in its home cage nesting box.

METHODS

The study was conducted during a 3-week period from June 2 through June 22, 1968, at the Southwestern Research Station of the American Museum of Natural History in Portal, Arizona. The Station is situated in a lightly wooded canyon at an approximately 6000-ft elevation beneath the peaks of the Chircahua Mountains. Temperature ranged from 32° to 97° F and humidity varied between 15 and 70%. About 10 miles down the canyon lies the Sonoran desert. The animals were all trapped in box traps (Havahart) from the vicinity of mounds in the desert, or from the station environs.

Animals were housed at the station laboratory under the natural outdoor light and dark cycle. All testing was conducted in the laboratory under approximately outdoor temperature and humidity (medians 82° F, 18% humidity). For the arena testing, moderately bright artificial light was produced by three double overhead fluorescent tubes. Light meter readings for reflected light in the arena ("open field") were 15.0–15.5 on "Luna six" photometer scale during the daytime testing and 14.3–14.6 at night when no light was entering the laboratory windows. Daytime outdoor readings at the station were: shade on grass, 15.5; sand in shade, 16.0; and in the sun, 20+. Each species was tested during its natural active period within the light dark cycle and basal rates were recorded during the inactive period, for that species.*

Housing and Handling Conditions

All animals were transferred from traps and cages by encouraging them to move from one container to another via a narrow alley or by "cupping" under an inverted clear plastic jar. All laboratory housing was in standard 8 × 10 × 8 in. rack cages with solid sides and back, and with mesh bottoms and fronts. A small cardboard nesting box with cotton, a supply of grain, lettuce and a water bottle were supplied for each animal.

Stimuli

The test arena was of plywood, painted flat white, measuring 36 in. on one side and 30 in. high. The subjects were introduced into this arena in a standardized manner from a specially designed metal starting box (8 × 4 × 8 in.) designed so that the four sides fell outward when the top was removed. A stylized hawk silhouette, cut from cardboard and mounted at the end of a long metal rod was brought slowly over the rim of the box and then plunged at the subject. The noise was generated by forcefully slapping two flat surfaces of wood together. In most cases a 4-ft king snake, kept without food for 1–3 weeks, was used as a predator stimulus. A 5-ft gopher snake was occasionally used. Both snakes had been maintained on live mice (Peromyscus) until 2 weeks prior to our experiments. The stimuli were always presented in the above order and no attempt was made to vary systematically the order of presentation of stimuli due to the small number of subjects in most species.

Recording and Implantation

Electrode implantation was performed under light ether anesthesia. An area on the dorsum of

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*Kangaroo rats, wood rats, grasshopper mice and deer mice are nocturnal or crepuscular while ground squirrels and Western chipmunks are diurnal.

the animal at the base of the neck and above the forelegs was clipped to 1–2 mm hair length. Two electrodes fashioned from Formvar-coated magnet wire (30 gauge) were placed under the skin, one originating above the sacral spine and the other, over the right thorax. Five to ten millimeters of insulation was scraped off the ends of the wires, thus determining the location from which recordings were made. Both insulated portions were passed subcutaneously to emerge at the shaved area where subminiature Amphenol pin connectors were crimped to them. Dental cement was then applied, embedding both electrode pins and hair roots, affixing the whole to the skin of the animal with considerable strength. Good recordings were obtained as long as 10 days after implantation. From this electrode placement, EKG, spinal EMG and impedance pneumograph (respiration) recordings can be made. A Grass Model 5 Polygraph was used with an impedance pneumograph preamplifier.* With this method, respiration cannot be reliably recorded during vigorous activity of the animal. Except for rare instances, at least a day was allowed to elapse after implantation before the animal was tested. The shortest time was 8 hr.

Behavioral observations were noted directly on the polygraph paper. Sixteen-millimeter film was utilized to record behavior in the testing situation on at least 2 subjects of each species, for illustrative purposes and later study.

Procedure

On the day of testing, the animal was removed from its home cage by cupping, and was dropped into a can with ether-soaked cotton. As soon as the animal became manageable, the leads were attached to the implanted electrode pins, the animal was placed in the metal starting box, and the leads suspended overhead, under light tension. Ninety minutes were then allowed for the subject to recover from this momentary anesthesia and to adapt to his new surroundings. At the end of this period, a 1–2 min recording was made, from which were taken the "start-box" cardiac and respiratory rates. The start box was then placed in the center of the "open-field" arena and 1–2 min allowed to elapse before the top was suddenly plucked from the start box, allowing the walls to fall abruptly outward. At least 5 min of recording and observation were then made, longer if immobility persisted. The other stimuli were then introduced at approximately 2 min intervals and the test concluded with the cupping and removal of the animal from the open field. The loud sound was administered as a single discrete stimulus lasting only a fraction of a second, while the silhouette and snake were presented for at least 2 min and longer if immobility persisted. Brief anesthesia induction was repeated to allow detachment of leads and the animal was replaced in its home cage. Several days later, the animal was again anesthetized, this time during its natural sleeping period, leads were attached, and the animal was returned to its home cage. Basal rates could then be recorded during sleep, several hours later. It was found that animals rarely chewed leads attached during their inactive period. During their active period in the start box, overhead suspension of the leads under light tension usually prevented it.

Animals from each species were also tested without the brief ether anesthesia, implantation or lead attachment, to check against gross differences in behavior which could have been attributable to these procedures alone. A wood rat, a ground squirrel and a chipmunk were also tested under the open sky, outside the laboratory.

Subjects

Thirty-one subjects of six different species were tested (Table 1). Species identification was often simple. Where any doubt existed, the animal was sacrificed and the skull taken for identification by Dr. Sydney Anderson of the Department of Mammalogy at the American Museum of Natural History. Seven skulls were so identified. The species studied were the kangaroo rat (*Dipodomys*—both *merriami* and *spectabilis*), the spotted ground squirrel (*Citellus spilosoma*), the western chipmunk (*Eutamias dorsalis*), the wood rat (*Neotoma*), the deer mouse (*Peromyscus*) and the grasshopper mouse (*Onychomys leucogaster*).

RESULTS

Behavioral Observations

Sudden, prolonged immobility was surprisingly common among the animals captured, under the conditions of testing. Usually sudden exposure to the testing arena itself when the sides of the box fell, was sufficient to induce periods of immobility in excess of 5 min. A few animals remained active until another stimulus was employed Occasionally the test had to be

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*E & M Instrument Co, Houston, Tex.

Table 1. Incidence and Duration of Immobility in Species Tested

Species	No.	Day of captivity tested		Duration of immobility (min)*		Effective stimuli†			
		Median	Range	Median	Range	Arena	Silhouette	Noise	Snake
Chipmunk									
First tests	13	3	1- 8	5+	3-19+	10	3		2
Subsequent tests	9	6	3-13	7+	3-25+	7			
Deer mouse									
First tests	5	1	1- 9	0.5	0.2-1.5				
Grasshopper mouse									
First tests	3	1	1- 1	6+	0.1-6+	2			
Ground squirrel									
First tests	3	1	1- 2	12+	4-40+	1	1		1
Subsequent tests	1	3		60+		1			
Kangaroo rat									
First tests	4	2	1- 5	0.2	0.1-0.6				
Wood rat									
First tests	3	2	1- 3	8+	2-10+	2			1
Subsequent tests	2	11.5	10-13	6.5	6-7	2			

+, observations interrupted while animal was still immobile; not a spontaneous termination of immobility.

* Refers to duration of longest single period of immobility.

† The first stimulus administered that was found to be effective in eliciting a period of immobility longer than 2 minutes' duration.

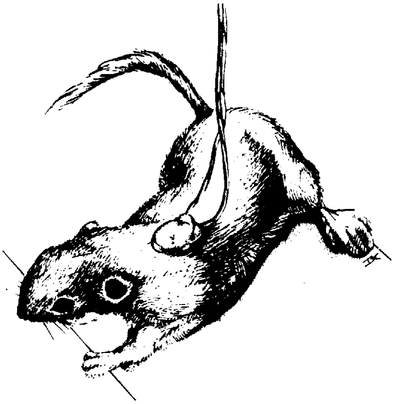

Fig 1. Typical posture of sudden prolonged immobility. This female ground squirrel remained motionless in this posture for 40 min. Implanted electrodes and attached leads are illustrated.

terminated after the animal remained motionless in a single pose for as long as 60 min. This behavioral characteristic was strongly related to species, as is evident in Table 1. None of the 4 kangaroo rats or 5 deer mice remained motionless for more than 1½ min and 21 of the 22 rodents of the four other species evidenced at least a 2 min period of immobility.

As soon as the start box was opened, the ground squirrels and chipmunks characteristically struck awkward positions in the center of the arena as if stopped in midmovement by the single frame of a moving picture strip (Fig 1). Often legs, tail or head were stiffly stretched at an unusual angle to the body. What appeared to be a fine, high frequency tremor of the whole body was actually the extraordinarily high respiratory rates characteristic of this state (200–400/min). The wood rats and one of the grasshopper mice darted first to the side or corner of the arena and assumed a crouching position. Rigidity or tension in the musculoskeletal system did not appear to be widespread or excessive. Spinal EMG in all cases was at or near levels recorded during basal conditions.

Because of the unexpectedly long periods of immobility and the time pressure on some days to test a number of animals, many episodes of immobility were terminated after varying time intervals, by moving on to another stimulus, or removing the animal from the test arena. (Time figures for such periods are followed by + in Table 1.) It is of course impossible to say how long these periods might have continued, but judging from the few animals who spontaneously terminated immobility, this would be found to be highly variable: for chipmunks, the most-studied species, these spontaneous terminationss ranged from 2 to 25 min after onset. For the same reason, it is not possible to say from our data whether immobility duration is related to recency of capture, frequency of testing or time of day tested (see Discussion). An understanding of these relationships will await parametric studies designed with them in mind.

Eight subjects were given more than one test (subsequent tests, Table 1) and there was no evidence of any striking tendency to decreased reactivity, even on the third repetition.

At least 1 subject of each species was tested without previous electrode implantation, or the brief anesthesia necessary to attach leads, and no differences in behavior were observed from those previously implanted and with leads attached. Five tests on 4 chipmunks were performed in this way and the duration of immobility ranged from 3 to 25 min, with a median of 5 min, comparable figures to those implanted and tested with leads attached.

Table 1 indicates that the hawk situation and the snake were occasionally effective in cases where the arena alone was insufficient to induce immobility. It should *not* be concluded, however, that the specific characteristics of the silhouette and snake were alone responsible, since it was found that close approach by the experimenter or a nonspecific cardboard cutout seemed equally effective in reinstituting immobility in susceptible individuals where activity had resumed.

The silhouette, noise and snake were as ineffective as the initial sudden exposure to the arena in eliciting prolonged immobility in kangaroo rats and deer mice. In the other four species, these stimuli were usually administered to animals which were already immobile. In such cases, there was always some slight evidence of startle, such as a momentary head movement, flattening of the ears, twitching of the vibrissae, and only rarely a gross change in body position with a quick resumption of prolonged immobility in a new position. In those instances when the animal was active prior to the stimulus, immobility was resumed following the stimulus in 9 of 11 instances.

The snake showed immediate orientation toward the rodent in the test arena. Ten of 25 animals exposed to the snake in the arena remained immobile until the snake inched its way to within a foot of the rodent. Nine of these 10 were from a total of 18 immobility-prone animals: 2 ground squirrels, 5 chipmunks and 2 wood rats. Both chipmunks and ground squirrels remained immobile, despite the snake curling under and around their bodies. The snake, however, did not ingest any of the rodents, but rather, moved away after a minute of this close investigation. The other animals reacted with hyper-alert orientation toward the head of the snake with rapidly alternating approach and withdrawal locomotor behavior.

Cardiac and Respiratory Regulation During Sudden Immobility

In Tables 2 and 3, a comparison is made between cardiac and respiratory rates under the different test conditions for the 23 subjects of the six species on which full physiologic recordings were available. Basal and start box conditions represented steady states (see Procedure section) from which 1-min recordings were taken. Little or no variability over time occurred in these tracings. Cardiac and respiratory rates were calculated from 6–15 sec samples of the lowest rates from these recordings. Medians of these individual values are presented for each species in Tables 2 and 3. The activity condition in these tables includes only heart rate because movement artifact obscured the impedance pneumograph recording. Heart rate was quite variable during activity but for the purposes of defining the full range of heart rate regulation, a 6-sec sample was taken from the highest heart rates observed during activity for each animal. For those animals exhibiting prolonged immobility, a near steady state condition was achieved, since a minimum of 1½ min without movement was required and immobility frequently exceeded 5 min. In most animals, heart rates were quite stable, but since some variability occurred, heart and respiratory rates were always calculated from the 6–15 sec of lowest rates during the first and third minutes. Those animals which failed to show prolonged immobility did show intermittent periods of inactivity throughout their time in the open arena. The lowest rates observed during such periods was calculated from 6–15 sec samples as before, and listed as Inactivity for comparison with the Immobility rates.

The main findings were those for species showing prolonged immobility (Table 2);

heart rates during that behavior were remarkably low—in three of four species, lower then the basal rates. Respiratory rate during immobility, on the other hand, was extremely high with median rates ranging from one and one half to five times basal rates. For species not showing prolonged immobility (Table 3), heart rates during periods of inactivity in the test arena were consistently higher than basal levels, paralleling the increased respiratory rates. This was true for a species with high basal heart

Table 2. Cardiorespiratory Measures for Species Showing Prolonged Immobility

					Immobility		
Species	Sex	No.	Basal (HR/RR)*	Start box (HR/RR)	First min (HR/RR)	Third min (HR/RR)	Active peak (HR)
Chipmunk	F	4	225/41	210/83	255/235	220/135	420
	M	4	245/63	280/120	365/360	350/150	505
(juvenile)	M	1	550/90	410/60	380/220	580/300	610
Grasshopper mouse	F	2	420/115	285/100	280/180	305/180	470
Ground squirrel	F	2	215/33	210/75	150/140	170/105	310
	M	1	170/60	170/70	150/160	200/120	300
Wood rat	F	2	245/105	250/105	225/240	230/240	315
	M	1	190/90	140/90	160/170	160/170	
MEDIAN DIFFERENCES FROM BASAL RATES							
Heart rate		17		0	− 20	−15	+130
p†				NS	NS	NS	<0.01
Respiratory rate		17		+20	+140	+90	—
p†				NS	<0.01	<0.01	—

HR, heart rate; RR, respiratory rate.

* All rates are medians.

† By Wilcoxon Signed Ranks Test.

Table 3. Cardiorespiratory Measures for Species Not Showing Prolonged Immobility

					Inactivity		
Species	Sex	No.	Basal (HR/RR)*	Start box (HR/RR)	First min (HR/RR)	Third min (HR/RR)	Active peak (HR)
Deer Mouse	F	3	420/200	500/160	520/360	520/160	660
Kangaroo Rat							
D merriami	F	2	280/115	260/110	360/270	315/180	370
D spectabilis	F	1	160/50	170/75	320/180	360/140	400
MEDIAN DIFFERENCES FROM BASAL RATES							
Heart rate		6		+20	+ 95	+65	+225
p†				NS	<0.05	<0.01	<0.05
Respiratory rate		6		0	+170	+50	
p†				NS	<0.05	<0.01	

* All rates are medians.

† By Wilcoxon Signed Ranks Test.

rates (deer mice) as well as for one with low basal rates (kangaroo rats). This difference in change values for cardiac rate between the species showing prolonged immobility (Table 2) and those which did not (Table 3) was significant beyond the 1% level, while respiratory rates did not differ ($p > 0.1$).* No statistically significant differences were found between the two groups of species in basal heart rates or in the other change values for either heart rate or respiratory rate.

The two groups of species also did not differ in their response to the start-box adaption. The pattern presented in this situation was one of relatively low cardiac and respiratory rates for all species.

Figure 2 presents the picture, graphically, for a species which showed sudden prolonged immobility (the spotted ground squirrel) and for one that did not (the kangaroo rat). Note the dissociation of cardiac and respiratory function during the immobility response in contrast to the concurrent cardiac and respiratory changes characteristic of inactivity in the species that failed to exhibit the immobility response.

There were enough chipmunks in the sample to allow a comparison of the two sexes. One animal was an immature male and the remaining 8 were evenly divided according to sex. Table 2 shows cardiac and respiratory rates for the two sexes of chipmunk over the conditions studied. The males increased their heart rate from basal levels to a greater degree than females during immobility and during peaks of activity ($p < 0.05$).* Basal levels for both cardiac and respiratory rates as well as all other change values did not differ significantly.

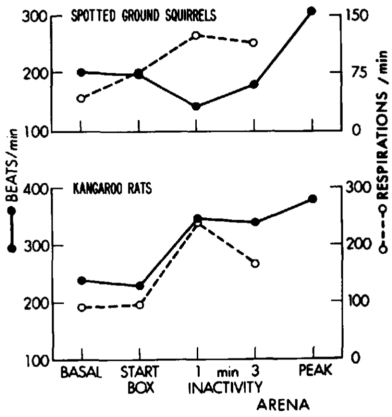

Fig 2. Comparison of cardiac and respiratory rates of two species showing difference in cardiac rate control during inactivity in test arena. Ground squirrels showed sudden prolonged immobility while kangaroo rats did not. N=3 for each species.

As described above, the silhouette, noise and snake were usually presented to animals already immobile, although always at least 3 min after the onset of immobility. The majority of subjects showed physiologic responses to these stimuli although behaviorally they were hyporeactive. Table 4 lists the number of subjects showing the different possible patterns of cardiac and respiratory responses to these stimuli. A response was defined as a clearcut deflection from stable baseline of at least 15% in magnitude immediately following stimulus onset. A large number of subjects showed biphasic or minimal responses. Among the directional responses, heart rates fell while respiratory rates rose ($p < 0.02$).† The recordings on subjects which were active prior to the stimulus either showed the characteristic physiologic responses of prolonged immobility following the stimulus or the subjects remained active (kangaroo

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*Mann-Whitney U tests.

†Sign test.

rats and deer mice). Activity artifacts in these tracings prevented a complete analysis of physiologic responses.

Cardiac Arrhythmias

To our surprise, transient cardiac arrhythmias occurred in the majority of the animals at some point during the testing procedures. A detailed electrocardiographic study was not planned, and although a single EKG channel was recorded at all times, the paper speed was slow (5–10 mm/sec), consistent with the long duration of the experiments and the primary interest in heart and respiratory *rate* parameters. However, irregularities of rate could be readily detected, and brief periods of faster paper speed (25–50 mm/sec) were

Table 4. Types of Cardiac and Respiratory Responses to Stimuli Presented During Prolonged Immobility

Stimuli	Basal rate	Minimal	Biphasic	Increase	Decrease
Silhouette	HR	7	6	0	6
	RR	4	5	9	0
Noise	HR	8	11	1	5
	RR	9	4	5	2
Snake	HR	3	1	0	12
	RR	3	0	9	3
Totals*	HR	18	18	1	23
	RR	16	9	23	5

* The number of subjects whose respiratory rate recordings were technically adequate was slightly smaller than that for heart rate recordings.

Table 5. Incidence of Arrhythmias in the Different Species

		Arrhythmia		Percent showing arrhythmia	No. of episodes of arrhythmia
Species	No.	Total no.	No., sex		
		IMMOBILITY PRONE			
Chipmunk	9	6	2, M 4, F	67	19
Grasshopper mouse	2	2	2, F	100	5
Ground squirrel	3	1	1, F	33	3
Wood rat	3	3	1, M 2, F	100	9
Totals	17	12	3, M 9, F	71	36
		NOT IMMOBILITY PRONE			
Deer mouse	3	1	1, U*	33	1
Kangaroo rat	3	0	—	0	0
Totals	6	1	1, U	17	1

* Unidentified sex.

run to allow the analysis of EKG wave form necessary to characterize the arrhythmia. In this study, disturbances of conduction with regular rates could be missed (eg, tachycardias) as well as disturbances hidden by movement artifacts during bursts of strenuous activity.

Five different forms of abnormal conduction were observed and these occurred in five of the six species (Table 5). Arrhythmia was seen in 56% of the 23 subjects. The four species exhibiting prolonged immobility, however, had a markedly higher incidence (71%) than the other two species not showing this behavior (17%) ($p < 0.03$).* Only the kangaroo rats failed to show arrhythmia. All the episodes occurred during inactivity and often were dispelled with movement and an increase in cardiac rate. Most of the episodes (15) occurred during periods of sudden prolonged immobility elicited by exposure to the arena itself, 11 were observed in the start box, and only occasional episodes were observed in other situations (Table 6). The occurrence of arrhythmias did not differ in the two sexes; the apparent preponderance of females (Table 5) merely reflects the proportion of females in the test population.

The most common abnormality was second degree atrioventricular block—ie, an intermittent failure of propagation of the electrical discharge beyond the auricle, resulting in failure of ventricular contraction (QRS complex) after every second, third or fourth normally conducted beat. Figure 3C illustrates the EKG during this disturbance. The second most common arrythmia was the irregular slowing of impulse generation at the S-A node (sinus arrhythmia) (Fig 3A) with occasional sinus arrest and the appearance of an A-V nodal pacemaker (Fig. 3B). Third degree A-V block indicates that the block has intensified to a

Table 6. Types of Arrhythmia and Settings in which Episodes Occurred According to Species

Types of arrhythmia	Basal	Start box	Arena	Stimuli	Cup	Total No.
Sinus arrhythmia	Ground squirrel	Wood rat	Chipmunk	Wood rat (silhouette)	Deer mouse	5
Sinus arrest with escape beats	Chipmunk	Chipmunk Wood rat	Chipmunk Grass mouse Wood rat			9
A-V block, incomplete	Chipmunk	Chipmunk Ground squirrel Wood rat	Chipmunk Ground squirrel Ground mouse Wood rat	Wood rat (noise)	Grass mouse	14
A-V block, complete					Grass mouse	1
Ventricular ectopic beats	Chipmunk	Chipmunk	Chipmunk Wood rat	Wood rat (snake)	Grass mouse	8
Totals	4	11	15	3	4	37

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*Fisher exact test.

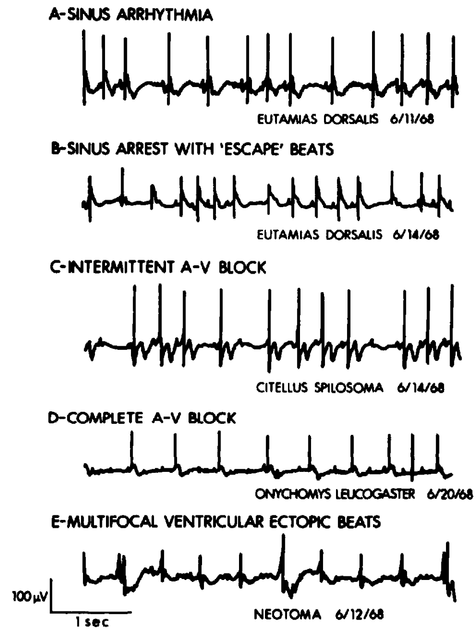

Fig 3. Examples of five major types of cardiac arrhythmias encountered.

complete dissociation between atrial and ventricular contraction, the origin of ventricular complexes shifting to the A-V node and functioning independently of the normal pacemaker and auricular contraction (Fig 3D). Finally, an ectopic focus may originate beats from within the ventricular muscle mass itself (distorted QRS complexes, Fig 3E). These ventricular ectopic beats (VEB) occurred intermittently, superimposed upon normal conduction or upon some other conduction disturbance.

States of Torpor and Feigned Death

Transient states of torpor were observed in 6 members of four species: chipmunk, deer mouse, ground squirrel and kangaroo rat. Typically, the condition was made apparent when the cage was opened slightly for food and water replacement and the animal failed to react. Upon investigation, the animal was found to be in a state resembling hibernation: cool to the touch when held in the hand, and profoundly unreactive, with a waxy flexibility of limbs. Several hours later, the animal would again show a normally intense startle reaction to slight opening of the cage and the usual predisposition of the wild rodent to lightning escapes if given the slightest chance. Recordings were made on 2 animals in the torpid state (Table 7) and showed extremely low heart rates in comparison to basal recordings after recovery.

A response resembling feigned death occurred in 3 animals upon cupping at the end of stimulation in the test arena. A clear plastic cup allowed the observations to be made. All animals initially jumped and struggled against the side of the cup; 3 animals suddenly collapsed inside the cup, sinking into a semicrouched position with eyes closed. The cup could be removed and the animal could be poked, even picked up by the tail without its making any movement. It appeared asleep or dead. Table 7 shows the extremely low heart rates and serious conduction disturbance seen in both grasshopper mice while in this state. The deer mouse showed the same behavior with heart rate near basal level, but without arrhythmia. This state terminated spontaneously after 40 sec–7 min with a sudden eruption into violent integrated escape behavior. Only the attached leads prevented the successful escape of these animals.

DISCUSSION

The results show that several species of recently captured wild rodents respond with prolonged immobility to sudden exposure in a plain wooden test arena. This state was characterized physiologically by low heart rate, high respiratory rate and a surprising frequency of cardiac arrhythmia. During this state, the animals were often unresponsive to stimulation, even to the close approach of a natural predator, the snake. Some species were far more prone to sudden prolonged immobility than others under the conditions of this study. It is worth noting that the species with the least tendency to inactivity in the test situation, the kangaroo rat, is exclusively nocturnal while the one with the most prolonged periods of immobility, the ground squirrel, is strictly diurnal. It seems most likely that this response is an adaptive characteristic for species with diurnal activity, serving to protect them from predators, such as the hawk, that rely predominatly on visual cues.

Judging from the physiologic measurements obtained, the organization of this psychophysiologic response is complex, involving both slowing and acceleration, in cardiac and respiratory systems, respectively. Although respiratory rate is greatly accelerated, its depth is so limited as to be almost imperceptible to the eye, perhaps contributing to the likelihood of the ani-

Table 7. Cardiorespiratory Measures During Torpor and Feigned Death

Species	HR	RR	Duration (min)	HR	RR
	TORPOR			RECOVERY BASAL	
Kangaroo Rat	30	18		210	50
Ground squirrel	100	85		200	30
	FEIGNED DEATH				
Grasshopper mouse	100*	120	7	410	110
Grasshopper mouse	290†	200	40	430	120
Deer mouse	400	120	6	380	80

* Complete A-V dissociation.

† Second degree A-V block.

mal being overlooked by a visually scanning predator. The bradycardia is most likely part of a complex cardiovascular response involving regional shifts in blood pressure and perfusion such as have been described in the dive reflex (10). Adams et al (11) have recently demonstrated a marked bradycardia in unrestrained cats during the seconds prior to responding to an attack by another cat. This slowing of cardiac rate was accompanied by inhibition of activity, decreased cardiac output and a marked constriction of the external iliac vasculature. During actual fighting these parameters all changed in the opposite direction.

Although transient cardiac deceleration in the human has been described by Lacey as a preparatory autonomic response related to subsequent performance (12) and by Graham as a component of the orienting response to novel stimuli (13), Obrist has shown that cardiac deceleration under these conditions is accompanied by a decrease in respiratory frequency and amplitude (14), rather than the marked increase in respiratory rate observed in the present study. Furthermore, the magnitude and duration of the bradycardia of prolonged immobility is on a wholly different scale from the small, transient fluctuations reported by the above authors, during orienting or preparatory responses in the human.

The response of feigned death was behaviorally and physiologically very similiar to prolonged immobility and was distinguished by (a) its sudden occurrence during active struggling, (b) the immediate closure of the eyes and (c) the impression of collapse conveyed to the observer by the movements through which the animal entered its immobile state. Field observations have documented the usefulness of such responses in allowing sudden escape from a predator lulled into inattention by the feigned death of the intended victim (1).

A human counterpart to these sudden immobilities may exist in vasovagal syncope or common fainting. Pronounced and prolonged bradycardia is a hallmark of this response in the human, and varying degrees of vagal arrhythmias can occur as well (15). The loss of consciousness in fainting is a consequence of the upright posture and is no longer present in the recumbent patient who continues to show the cardiovascular changes. Perhaps sudden immobility in the rodent is a phylogenetic precursor to which we have added the dimension of loss of consciousness by adopting the erect posture and the means to describe our subjective state.

The occurrence of torpor in some of the animals provided another form of prolonged immobility, also associated with profound decreases in heart rate but with decreased respiratory rate and probably body temperature as well. Torpor or estivation is understood to be a variant of hibernation of shorter duration, with a less pronounced drop in body temperature and an independence from seasonal and climatic factors for its initiation (16). Usually it is thought to be induced by a temporary decrease in food level or drought. It was observed in our subjects, despite abundant food, water and shelter, thus suggesting that the environmental dislocation of captivity was an important precipitant. Is it possible that a common neurophysiologic substrate mediates the acute responses of prolonged immobility and feigned death, while torpor and hibernation represent its chronic and most extreme expressions?

What might be the relationship between the prolonged immobility observed in the present study and the most familiar form of immobility, sleep? Other studies, which utilize rabbits during restraint-induced immobility (4), and the oppossum during feigned death (17), have reported an alert, desynchronized EEG; multiple unit recordings suggested active inhibition originating in the central core of the brain stem, but not in nuclei implicated in slow wave or paradoxical sleep. However, the periods of immobility induced by the methods used in those studies were of relatively short duration (2–3 min, with maximum of 8 min). In our studies, during pilot work, 3 chipmunks were tested during their inactive period, and 2 of the 3 showed an almost imperceptible, slow relaxation of the immobile posture after approximately 5 min. These animals gave every appearance of having made a gradual transition from immobility into sleep.

The significance of the numerous cardiac arrhythmias occurring under stress in these species is somewhat difficult to assess. Although certainly ominous in the human, it has been found that healthy horses show first and second degree heart block in resting ECGs (18). It is also possible that even the few seconds of exposure to ether, necessary for attaching recording leads to the implanted electrodes, could have sensitized the myocardium of susceptible species to parasympathetic effects. This would seem unlikely in view of the 90 min allowed for the animals to recover fully before testing and the generally benign effects of ether anesthesia on neurogenic arrhythmias in extensive experience with man, dog and rabbit (19).

The five types of arrhythmia noted in this study are thought to be parasympathetic in etiology and can all be experimentally elicited by stimulation of the vagus. Richter observed fatal cardiac arrest, also apparently mediated by the parasympathetic system, in wild Norway rats that were handled and tested in the laboratory (20). While none of our animals died during testing, 26% of those trapped died without apparent cause within the first week in the laboratory. Within the sample of 23, on whom physiologic recordings were obtained, 3 subsequently died; all of these had shown arrhythmias during the tests. Of the 10 which failed to show arrhythmia during testing, none died. The small number of deaths precludes statistical significance, but the facts suggested the hypothesis that for the newly trapped animal, the repeated and prolonged stress of captivity may repeatedly elicit immobility responses and/or torpor with prolonged vagal effects upon the cardiac conduction system. In the captive situation, the response is no longer adaptive because the predator does not go away after the response is made. Repetition with insufficient recovery between episodes may end in fatal cardiac arrhythmia.

SUMMARY

Sudden prolonged immobility is a prototypical behavioral response to perceived danger and is exhibited by many species of animals from insects to man. This study describes the elicitation of this response in recently captured wild rodents and some of the cardiac and respiratory changes which accompany it.

Thirty-one members of six different species were trapped in the Sonoran desert region of Arizona and tested in a field laboratory near the place of capture. Observations of respiratory and cardiac rate and EKG were made on a Grass Polygraph via light weight leads from previously implanted electrodes in unrestrained animals. They were all tested in their home cage nesting box and in a standard open-field arena where they were subjected to sudden visual and auditory stimulation as well as to a natural predator.

Periods of prolonged immobility ranging from 2 min to more than 60 min in dura-

tion were elicited in 21 members of four species. This behavioral state was accompanied by very low heart rates and a high incidence of cardiac arrhythmias. Nine members of two other species did not show prolonged immbolity, had increased heart rates during testing and a significantly lower incidence of cardiac arrhythmias. All species showed markedly increased respiratory rates during testing. Physiologic recordings were also obtained during feigned death responses and during transient torpor.

The adaptive value of these responses is discussed and the physiologic changes compared to those known to occur during syncope, sleep, expectation of attack and sudden death.

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