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Epilepsy and Behaviour of the Mongolian Gerbil: An Ethological Study

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CUTLER, M. G. AND J. H. MACKINTOSH. *Epilepsy and behaviour of the Mongolian gerbil: An ethological study*. PHYSIOL BEHAV **46**(4) 561–566, 1989.—Ethological procedures were used to compare behaviour characterizing seizure-sensitive and seizure-resistant gerbils and to examine motor components of their major convulsions. Seizure-sensitive gerbils showed less social investigation when encountering an unfamiliar resident than their seizure-resistant counterparts. Sequence analysis showed the motor components of major seizures to segregate into three largely independent groups comprising elements associated with clonic-tonic spasms, with subsequent extensor immobility and with returning abnormal activity which preceded the resumption of normal behaviour. In grade 4 and 5 convulsions, the motor components of clonic-tonic spasms included the elements "rigid upright posture," "foreleg treading," "fall over," "mouth spasms," Straub tail and opisthotonus which were not seen in grade 3 seizures. The durations of clonic spasms and extensor immobility were longer in seizures of grades 4 and 5 than in those of grade 3. The abnormal motor activity following extensor immobility was complex and unrelated to seizure severity. It is suggested that observational studies in epilepsy may contribute to our understanding of the underlying pathophysiological processes.

Gerbil Behaviour Social investigation Seizures Motor components

THE Mongolian gerbil *(Meriones unguiculatus)* exhibits reflex epileptiform seizures. These occur in response to a variety of stressful stimuli such as handling, unfamiliar environments, a blast of air or dropping from a height (13,28). Susceptibility is associated with a wide range of factors which include genetic predisposition (15), cerebrovascular abnormalities (26), synaptic ultrastructural changes in the hippocampus (21) and a midbrain benzodiazepine/γ-aminobutyric acid receptor deficit (20). Perhaps the most important aspect of gerbil epilepsy is its association with the hippocampal defect (22,23), since knife cuts through the perforant path in the hippocampus will completely inhibit epileptic activity in the seizure-sensitive gerbil.

Seizures of the gerbil have become popular as a model of human epilepsy and also have been used for antiepileptic drug evaluation (12, 14, 24). Severity of seizures is generally rated on a 0 to 6 point scale by the criteria described by Loskota *et al.* (15). These grades, based on initial motor manifestations of the seizure, have been shown to be related to the degree of spread of the paroxysmal epileptoid EEG activity that generally commences in the sensorimotor or nearby parietal cortex (16). However, the progression of motor patterns during the subsequent period of the seizure has received comparatively little study and there are conflicting accounts of the sequential arrangement of motor activities (12,15).

The techniques of ethology, which have been shown to provide a highly sensitive measure of behavioural activity in humans and animals (6, 9, 17), have been used in the present study to quantify motor components of the gerbil seizure, as well as to compare the behavioural characteristics of seizure-sensitive and seizure-resistant animals. Ethology, described as the "biology of behaviour," has found increasing application in psychiatry and psychopharmacology for accurate description of abnormalities in motor activity and social interaction. The ethological approach involves initial recording of motor acts and postures as they occur, and subsequent statistical analyses to identify interrelationships between these behavioural elements so that behavioural categories, which underlie the structure of behaviour, can be defined from the element groupings. Thus, the first step in the present investigation of gerbil epilepsy was to make a baseline description of its individual motor components. The second step was to examine the sequential relationships of these motor acts so as to produce an objective classification of seizure elements within recognizable groups. Finally, since comparatively little is known about the behavioural correlates of the "epileptic predisposition," an assessment was made of the spontaneous behaviour of seizure-sensitive and seizure-resistant gerbils.

EXPERIMENT 1

METHOD

Subjects and Housing

Male and female Mongolian gerbils *(Meriones unguiculatus)*, aged from 8–16 months, were employed. These had been bred for several generations in our laboratory, following their original purchase from Intersimian Ltd., Abington. As in the colony of Thiessen *et al.* (28), 25–30% both of males and of females were seizure-sensitive. Gerbils were housed in groups of 2–6 and given an ad lib supply of tap water and Oxoid breeding diet (Diet 41B)

TABLE 1

BEHAVIOURAL ELEMENTS USED IN ANALYSIS OF THE GERBIL SEIZURES

Element	Description
All types of clonic spasms (A)	Clonic spasms of discrete body areas such as head, forelegs and hindlegs, spasms of pinnae, whole-body spasms.
Jerk forwards (B)	Uncontrolled jerking or running forwards.
Head back (C)	Head arched back, often progressing to involve the whole spine, causing opisthotonus.
Rigid upright (D)	Rigid upright posture, held for a brief period prior to loss of balance.
Fall over (E)	Fall due to loss of balance.
On side (F)	Animal on back, on side or rolling over.
Foreleg treading (G)	Repetitive foreleg treading performed from a rigid upright or partial upright posture, during which the paws make no surface contact.
Mouth spasms (H)	Clonic spasms of mouth muscles.
Tail up (I)	Tail raised to a rigid vertical or curved upright position.
Crouch (J)	Composite of crouch (17); flattened crouch in which the body is rigidly extended, forelegs pushed forwards and hindlegs spread out laterally; and humped crouch in which the back or rear part of the body are raised whereas the head and thorax are flattened close to the substrate.
Eye blink (K)	Eyes blink, sometimes repetitively (17).
Ears flattened (L)	Pinnae flattened.
Squint (M)	Brief partial eye closure.
Vibrissae twitch (N)	Rapid whisker vibration.
Head turn (O)	Lateral head turns, often repetitive.
Head bob (P)	Vertical head movements.
Rotate (Q)	Rotate in tight circles guided by the forelegs.
Circle (R)	Locomotion in fixed circular pathways.
Catatonic pause (T)	A variety of rigid or semirigid 'held' postures in which the gerbil suddenly stops in the midst of activity.
Wash (U)	Wash, self-groom (9).
Explore (V)	Explore (9).
Scan (W)	Scan, partial upright posture (4,17).
Other nonsocial acts (X)	Composite of dig, scratch, footstomp, mark sawdust, scratch walls, roll (17).

supplemented with sunflower seeds and cabbage. Animals were kept in conditions of controlled temperature (22 ± 2°C) and lighting (dark period 6.00–18.00 hr).

Experimental Procedures

Prior to seizure testing, gerbils were housed in a dimly lit room for at least 1 hr. This was at the commencement of the dark phase in their lighting regime, when seizure susceptibility is reported to attain maximal levels (28). Seizures were elicited by lightly stroking each animal from head to tail for 30 sec under a 25-W lamp and then releasing it for 30 sec of free exploration in an unfamiliar cage. If no convulsions occurred, the same procedure was repeated once more. As soon as a major convulsion commenced, motor acts and postures were recorded as a spoken commentary on a tape recorder as in previous ethological experiments (3, 4, 6, 9, 17). Motor activity was simultaneously recorded by videotape, and the videorecordings were subsequently analysed by the same observer who was "blind" to the animal number under observation. The records from direct observation and observation of the videorecordings showed a high degree (95–100%) of comparability.

Seizure severity was graded by the criteria described by Loskota *et al.* (15). This system classifies seizures of grades 1 and 2 as twitching of the vibrissae and pinnae without or with motor arrest, grade 3 convulsions are characterized by myoclonic jerks, while clonic-tonic seizures are classified as grade 4 and clonic-tonic convulsion coupled with body roll are described as grade 5. Grade 6 convulsions are those which progress to death.

Motor Acts and Postures Characterising Gerbil Epilepsy

Table 1 lists and describes the 23 postures and motor acts observed during seizures of the gerbil. Elements have been listed

TABLE 2

DISTRIBUTION OF THE SIGNIFICANT TRANSITIONS IN THE SEQUENCE MATRIX

	Following Elements																							
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X
Preceding elements																								
A (Jerk)		*	*			*				*		+												
B (Jerk forwards)	*			+						+														
C (Head back)	*					*		*	+															
D (Rigid upright)	+	+					+																	
E (Fall)						+																		
F (On back or on side)	*		*					+					+											
G (Foreleg tread)		+		*	+										+					+				
H (Mouth spasms)	+	+					+		+															
I (Tail up)										+														
J (Crouch)	+										*		*	+	*	+								
K (Eye blink)										*														
L (Pinnae flattened)	+									*			+	+										
M (Squint)										+		+												
N (Vibrissae twitch)										*		+												
O (Head turn)							+			*							+		+	*	+	+	+	−
P (Head bob)										+										+				
Q (Rotate)																				+				
R (Circle)																				+				
S (Move backwards)																	+							
T (Pause)							+								*	+	+				+		+	
U (Wash)							+								+					*		+	+	
V (Explore)															+		+	+			+		*	
W (Scan)																	+			+	+	*		+
X (Other nonsocial)																						+		
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X

+ = chi-square >12 and <100.
* = chi-square >100.
A jerk; B jerk forwards; C head back; D rigid upright; E fall; F on back or on side; G foreleg tread; H mouthing; I tail up; J crouch; K eye blink; L pinnae flattened; M eye squint; N vibrissae twitch; O head turn; P head bob; Q rotate; R circle; S move backwards; T pause, often catatonic; U wash; V explore; W scan; X other nonsocial acts.

in the approximate order in which they occurred during a typical major seizure. These elements had been identified during preliminary studies of convulsions from 50–60 stock gerbils.

Sequence Analysis

The motor acts of 90 major seizures (ranging in severity from grade 3 to grade 5) were transcribed from audiotape onto a microcomputer by means of a data logging programme. Seizures had been obtained from 70 animals.

The frequency with which each seizure element was followed by each other element was then calculated and, so as to assess nonrandom occurrence of seizure elements, the resulting transition frequencies were converted to chi-square values using the method described by Grant (8). The threshold for significance was selected as an arbitrary but conservative chi-square value of 12. It is probable that the data did not exhibit complete stationarity and this may somewhat bias the results.

Seizure Durations

The duration of each seizure and the component parts of initial clonic-tonic spasms, subsequent extensor immobility and the period of returning but abnormal motor activity were subsequently recorded by a posture adder and timer used in previous behavioural studies (3).

RESULTS

Sequence Analysis

The pattern of the most significant positive transitions in major seizures can be seen from Table 2. This shows that the significant sequences segregated into three groups, the first comprising elements associated with the initial clonic-tonic spasms, the second being formed of the elements associated with "crouch" or extensor immobility and the third consisting of elements such as "head turn," "rotate" and "move backwards" which occurred during the period of returning activity. These element groups can be seen to be largely independent, although overlaps occur between the first and second groups with the elements "foreleg tread" (G) and "on side" (F) and between the second and third groups with the elements "head turn" (O) and "head bob" (P). The only element showing significant transitions to all groups is "foreleg tread" (G).

During the initial clonic-tonic spasms the "body jerks" commonly progressed to "jump forwards" or to "run forwards," as can be seen from Table 2. It was observed that such animals, when placed in a large enclosure, could cover considerable distances

TABLE 3

DURATION OF SEIZURES AND THEIR COMPONENT PARTS AT EACH GRADE OF SEIZURE SEVERITY IN GERBILS

	Grade: 3	4	5
n	40	39	11
	Duration, sec, mean ± SD		
Clonic spasms	16.7 ± 11.6	47.1 ± 13.7	47.8 ± 14.3
Flattened crouch	28.0 ± 47.2	88.2 ± 29.6	85.0 ± 41.7
Returning activity prior to normal behaviour	260.6 ± 156.1	162.8 ± 62.1	236.0 ± 108.9
Total duration of seizure	305.3 ± 141.3	298.1 ± 55.4	368.8 ± 99.1

with undirected running. In grade 3 convulsions, this running was terminated either by the sudden motor arrest of "crouch" or by further spasms. The undirected running by animals in grade 4 or 5 seizures ended either in clonic-tonic spasms in which the head was arched back or in a "rigid upright posture" accompanied, in most cases, by "foreleg tread." The animal then would fall to lie "on side" or "on back," showing violent clonic-tonic spasms accompanied by head arching and opisthotonus and in some animals by "tail-up."

All clonic-tonic spasms were abruptly terminated by the transition to the "crouch" of tonic immobility in which pinnae were flattened, forelegs pushed forward and the hindlegs spread out laterally. During this phase, which often was prolonged, crouching was associated with "eye blinks," repetitive twitching of the vibrissae, and in some cases with a brief spasm of partial eye closure termed "squint."

The occurrence of "head turn" and "head bob" marked the transition from the phase of extensor immobility to that of resuming motor activity. The pinnae were raised and the head and body were gradually lifted to a normal "crouch" or "sit." Behaviour displayed during the phase of returning activity was extremely variable, containing stereotyped sequences of slowly occurring normal and abnormal motor acts which were interspersed with periods of rigid or semirigid immobility. Thus, the element "head turn" was closely associated not only with "crouch" but also with "rotate," "head bob," "foreleg tread," "move backwards" and "catatonic pause" as well as with acts of normal nonsocial behaviour (Table 2). Gerbils appeared unresponsive to stimuli during the initial but not in the latter part of a "catatonic pause." A small proportion of the animals showed multiple seizures.

The ultimate return to truly normal behaviour frequently was abrupt and could be hastened by subjecting the animal to tactile or auditory stimulation.

Seizure Durations

Table 3 shows that the durations of clonic-tonic spasms and extensor immobility was significantly greater in seizures of grades 4 and 5 than in those of grade 3. There were no apparent differences between grade 4 and grade 5 convulsions in the length of clonic-tonic spasms and the subsequent immobile period. The period of returning activity was prolonged, and its duration bore no obvious relationship to the severity of seizures.

TABLE 4

CATEGORIES ADOPTED FOR THE DESCRIPTION OF BEHAVIOUR AND THEIR RESPECTIVE POSTURAL ELEMENTS

Category	Postural Elements
Nonsocial behaviour	Explore, upright scan, partial upright, jump, on bars, off bars. Wash, self groom, ventral groom, scratch, eat, stretch, shake, dig, scratch walls, lick walls, sawdust bathe, drum, rotate, substrate. Sit, crouch
Marking behaviour	Mark sawdust, roll, mark walls.
Social investigation and sexual behaviour	Attend, stretched attend, approach, investigate, nose, sniff chin, sniff, push under, ventral sniff, groom, crawl over, follow, huddle, push down, paw, mount, attempted mount, genital groom, crouch.
Flight	Flag, evade, retreat, flee, evasive jump, defensive crouch, circle away, lie on back, defensive sideways, defensive upright, freeze.
Aggression	Threat, thrust, attack, bite, chase, aggressive groom, offensive sideways, sidling, box.

EXPERIMENT 2

METHOD

Subjects and Housing

Adult male Mongolian gerbils, aged 5–16 months, were employed for the behavioural studies. These animals were from the same colony as those used in Experiment 1 and were maintained under identical housing and lighting conditions. Behavioural testing was performed between 9.30 and 16.30 hr.

Experimental Procedures

Behaviour shown by seizure-sensitive gerbils in encounters with unfamiliar resident animals was compared with that shown by seizure-resistant gerbils. This resident-intruder paradigm was employed as optimal for the detection of timidity in gerbils of these two groups. The seizure-sensitive animals were those which consistently showed convulsions in response to handling whereas seizure-resistant animals were those which failed to convulse. At 3 days prior to the behavioural assessments, all gerbils to be used as intruders were tested for their susceptibility to handling-induced convulsions by means of the procedures outlined in Experiment 1. Since gerbil epilepsy is characterized by a refractory period of approximately 7 days (28), this protocol prevented convulsions from occurring during the behavioural tests. Resident gerbils were housed individually in transparent observation cages ($61 \times 25 \times 25$ cm) for 7 days and had free access to rat cake and water until the time of social encounters, when water bottles and food were removed.

Behaviour shown by the gerbils during 5-min resident-intruder interactions was recorded by two observers, one for each animal, using the profile of acts and postures listed in Table 4 (4). The spoken commentaries were transcribed onto recording disc for

TABLE 5

BEHAVIOUR OF SEIZURE-SENSITIVE (SS) AND SEIZURE-RESISTANT (SR) GERBILS DURING DYADIC ENCOUNTERS

	Mean Frequency (±S.E.)		Mean Duration (±S.E.), sec	
Group	SR	SS	SR	SS
n	28	30	28	30
Behavioural Category				
Non social behaviour				
Explore	54.2 ± 3.2	61.6 ± 3.0	103.3 ± 4.2	103.1 ± 5.6
Scan	48.6 ± 3.4	55.3 ± 3.1	110.0 ± 6.6	121.0 ± 4.8
Other nonsocial	12.6 ± 1.5	13.0 ± 1.3	28.7 ± 3.1	30.4 ± 5.0
Social and Sexual investigation				
Attend	11.2 ± 0.9	10.5 ± 0.9	11.3 ± 1.1	10.6 ± 1.4
Other social	24.1 ± 2.3	18.4 ± 2.0*	45.2 ± 5.6	30.8 ± 3.7*
Marking	0.5 ± 0.3	0.2 ± 0.1	0.5 ± 0.3	0.3 ± 0.1
Aggression	1.3 ± 0.5	0.6 ± 0.2	2.2 ± 1.9	1.6 ± 1.2
Flight	1.3 ± 0.5	0.8 ± 0.3	2.6 ± 1.3	2.5 ± 1.3

*$p<0.05$ between seizure-resistant (SR) and seizure-sensitive (SS) gerbils by the Mann-Whitney U-test.

analysis by microcomputer of the frequency and duration of each behavioural element and of the categories of nonsocial behaviour, social and sexual investigation, marking behaviour, flight and aggression. Data were recorded as the means for each group and the significance of differences between the groups was estimated by the nonparametric Mann-Whitney U-test.

RESULTS

Table 5 shows that although there were no differences between seizure-sensitive and seizure-resistant gerbils in occurrence of the act "attend," seizure-sensitive gerbils did show a significantly lower frequency and duration of active social and sexual investigation than their seizure-resistant counterparts. There was a small increase in the frequency of "explore" and "scan" among the seizure-sensitive animals but this failed to reach statistical significance ($p=0.1$ by the Mann-Whitney U-test), and no other behavioural differences between the groups were detectable. The resident gerbils showed no differences in behaviour when encountering seizure-sensitive and seizure-resistant intruders. Levels of agonistic behaviour were low in both residents and intruders.

GENERAL DISCUSSION

Convulsive behaviour in the gerbil most commonly occurs in response to stressful stimuli or situations (12,15). Indeed, habituating gerbils to specific stress-inducing stimuli will reduce their seizure incidence (18) as will the rearing of gerbils under standard "exposed" laboratory conditions rather than in a sheltered environment (5). Little is known of the incidence of epileptic behaviour among wild populations of gerbils, although it has been suggested that there is a link between convulsions and predator confusion and hence escape mechanisms in some rodent species (1,2). It is not known if seizure sensitivity among gerbils in the wild protects from predator attack to aid survival, although this might occur, since there was uncontrolled running followed by immobility during convulsions among the gerbils in our study. Loskota *et al.* (15) noted that drumming and behavioural elements of the startle response can precede the occurrence of a gerbil seizure, while Thiessen *et al.* (28) suggested that susceptibility to seizures in gerbils was linked to the level of arousal and increase of stimulus input. The present finding that seizure-sensitive gerbils were characterized by lower amounts of active social interaction than their seizure-resistant counterparts when in the presence of an unfamiliar resident animal might represent an increase of timidity. Social interaction between rodents is reduced by anxiogenic compounds and enhanced by anxiolytic drugs (7,27), although many other factors can obviously influence social interaction among gerbils (25).

Seizures of the gerbil are short lasting. Those induced in our studies showed an overall duration closely comparable with that of convulsions of similar grades in gerbils of the seizure-sensitive WJL/UC strain (15). In our studies, the duration of spasms and of tonic immobility was longer in seizures of grades 4 and 5 than in those of grade 3. On the other hand, there was little difference in the duration of spasms and immobility in grade 4 and 5 convulsions, which suggests that the criterion of loss of balance used to distinguish these two grades may not be a true index of greater seizure severity. The period of abnormal activity at the end of the seizures was prolonged and independent of seizure severity. In future studies, it may be better to exclude the period of abnormal activity when measuring the overall duration of seizures.

Most published descriptions of gerbil epilepsy in the laboratory agree that their first external manifestation is a cessation of motor activity accompanied by spasms of the whiskers, eyelids and pinnae, progressing to localized myoclonic jerks with body flattening (12,16). The present results based upon sequence analysis show that motor manifestations of seizures in the gerbil form three distinct groups which are largely independent, clonic-tonic spasms, extensor immobility and a period of returning but abnormal activity. During the initial clonic-tonic spasms, the gerbil's cortical EEG has been shown to resemble that of human grand mal epilepsy (15, 16, 19). The period of extensor immobility is associated with EEG depression. The third phase of the gerbil's seizure, with its stereotyped and abnormal motor activity preceding the return of EEG activity and behaviour to preictal levels, differs from human grand mal epilepsy in which automatic behaviours are rarely present (10,11).

Loskota and Lomax (16) noted that the motor manifestations during the initial clonic-tonic phase of seizures depended on the degree of spread of paroxysmal epileptoid EEG activity. In severe seizures of grades 4 and 5, this affected the hippocampus and subcortical structures as well as the cortex. The adoption of an upright posture with foreleg treading and the subsequent loss of balance with head arching and opisthotonus seen in grade 4 or 5 seizures in the present experiments may arise from electrical excitation of the limbic areas. It has been suggested that the rigidity characterized by "extensor immobility" during the subsequent period of EEG depression might arise from cut-off of the inhibitory controls from higher regions of the brain over medullary neurons regulating the extensor tone of muscles (10). The slowly occurring stereotyped sequences of behaviour interspersed with catalepsy, characterizing the resumption of behavioural activity at the end of the immobile phase of the seizure may once again reflect the involvement of limbic structures which can initiate the occurrence of automatismic behaviours. The pattern of activity during this phase was extremely varied, as also has been noted by Kaplan and Miezejeski (12).

Much of the experimental research in epilepsy has hitherto been pharmacologically orientated. With current advances in our understanding of the interrelationships between pharmacology, biochemistry, physiology and behaviour, further insights into the underlying processes in epilepsy are likely to arise from more detailed and analytic observation of the behavioural components of preictal, ictal and postictal states in animal and human epilepsy, as well as from the biochemical and pharmacological studies. Such an approach should eventually lead to a better understanding of the pathophysiology and hence to a better management of the seizure itself.

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