1). Thus, for example, synchronization of 12 to 13 hertz occurred during similarly violent behavioral responses, while 9- to 10-hertz synchronization appeared during well-controlled escape or withdrawal behavior. Perhaps because this behavior was acquired on the first 15-minute trial of testing, we noticed no difference in hippocampal activity in response to dorsal midbrain stimulation between early and late trials. Within a 15-minute trial, however, we observed a waning of the behavioral response which was directly related to a reduction of hippocampal synchronization frequency.

Rebound effects were not apparent either following termination of individual stimuli or following successful movement to escape stimulation. Instead the synchronization occasionally continued with a slight decrease in frequency after stimulus offset (see 603, Fig. 1).

Three animals were not used in this study because one animal was accidentally killed with an overdose of ether, and two developed stimulus artifact in the hippocampal records which made the interpretation of the electroencephalographic records difficult. As in the freely moving condition, aversive midbrain stimulation elicited hippocampal synchronization during paralysis (Fig. 2). The relation between intracranial stimulus intensity and frequency of synchronization seen in the behavioral situation was also maintained under paralysis. It may be concluded, therefore, that the general features of the results obtained in the freely moving animal were present in the paralyzed subject. There was, however, a reduction in synchronization frequency during paralysis. Thus, for the same stimulus intensity applied to the freely moving rat, the frequency of hippocampal synchronization during curarization was reduced by 2 to 4 hertz. Tactile stimuli which normally produced synchronization of 7 to 8 hertz in the freely moving animal now produced synchronization of 5 to 6 hertz. Since *d*-tubocurarine is generally considered to have no direct central effects (*8*), this reduction in hippocampal synchronization frequency was unexpected, and, to our knowledge, has not been previously reported. Possibly the reduction in frequency was related to the joint effects of *d*-tubocurarine on blood pressure (*8*), proprioceptive feedback (*9*), and behavioral variables related more directly to execution of the aversive response itself.

Our results limit the generality of the view of Grastyan *et al.* (*2*) correlating push (aversive) behavior with hippocampal desynchronization. In the present study, hippocampal synchronization, not desynchronization, consistently occurred during aversive stimulation. In contrast to the results of Grastyan *et al.* (*2*), hippocampal desynchronization did not occur in the present study while the animals were withdrawing from the aversive stimulus. It is worth emphasizing, too, that the consistent occurrence of synchronization during aversive stimulation questions the view that synchronization occurs primarily during pull (approach) behavior or rewarding stimulation. Apparently, then, the biphasic character of hippocampal activity may not differentiate between aversive (push) and rewarding (pull) motivational situations. Our present speculation is that hippocampal synchronization correlates with the processing of inputs, rewarding or aversive, and that desynchronization in hippocampus correlates with the processing of outputs (*4, 5*). Further discussion of this view awaits the collection of data.

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## Optomotor Responses to Monocular Stimulation: Relation to Visual System Organization

Abstract. *Results of tests on 4 mammalian, 19 reptilian, and 17 avian species confirmed the prediction that lack of optomotor response to monocular optokinetic stimulation in one of the two horizontal directions would correlate with afoveate retinal organization, whereas consistent optomotor responses to monocular stimulation in either horizontal direction would correlate with foveate organization.*

Optomotor reflexes are mechanisms by which animals hold their eyes in a stable orientation relative to the visual surroundings, regardless of changes in head and body position. This is important for maintenance of perceptual orientation and acuity. Optomotor responses of animals from arthropods (*1, 2*) through anthropoids (*3–5*) have been studied by placing the animal in a rotating cylindrical screen: As the screen turns, the animal moves in a manner which reduces or eliminates retinal movement of the screen's image (*2, 6*). If the animal turns only its head and eyes, without substantial body rotation, then turning in the direction of stimulus movement is interrupted at intervals by brief rapid "recovery" movements in the opposite direction, producing an oscillatory ("nystagmoid") pattern of head or eye movement (or both) termed optokinetic nystagmus (OKN). In primates the OKN pattern normally will be the same no matter which eye is stimulated (*5–7*), but this is not the case for all mammals: a "unidirectional" response pattern has been described in rabbits (*5, 6*) and guinea pigs (*5, 8*). In these animals, if one eye is occluded, OKN is elicited when movement of the stimulus pattern is directed across the anterior visual field from the uncovered eye toward the covered eye (u→c), but it is minimal or absent when movement is in the reverse direction (c→u). Thus, if only the right eye is stimulated, optomotor response will be elicited when the cylinder turns to the left but not when it turns to the right; if the left eye is stimulated, response will occur only when the cylinder turns to the right. This type of unidirectional response pattern has also been reported for domestic pigeons (*9*) and chickens (*10*).

The unidirectionality observation [as well as those concerning effects of central nervous system damage on OKN in the normally bidirectional primates (*4, 7, 9*)] may be placed in correspondence with certain findings concerning functional neuroanatomy of OKN. These findings demonstrate that horizontal OKN with fast phase toward a given side is under direct control from the contralateral cerebral hemisphere (*7*) or superior colliculus (*8, 9*). Thus, OKN with fast phase to the left is under immediate control from the right cerebral hemisphere (monkey) or right superior colliculus (guinea pig or pigeon). It has therefore been proposed that unidirectionality is associated with complete crossing of the visual pathways (*5, 10*). Animals previously found to have unidirectional optokinetic responses (rabbit, guinea pig, pigeon, chicken) do in fact have complete or nearly complete crossing of the visual pathways at the optic chiasm (*11*), whereas the bidirectional animals (primates and carnivores) have a large proportion of uncrossed optic fibers. It would follow that the monocular optokinetic reponses of inframammalian vertebrates should be overwhelmingly unidirectional, since their optic pathways are said to be entirely crossed (*11*).

But such suggestions tell us very little about the adaptive significance of unidirectionality. What role does this optomotor response characteristic play in the organism's interactions with its environment? A hypothesis concerning the adaptive role of unidirectionality (*12*) was formulated previous to this series of observations. The hypothesis rested upon a difference between the ways in which foveate and afoveate animals deal with relative movement of the visual environment during forward locomotion. Whereas foveate animals can move their eyes to match the relative motion of any environmental object, afoveate animals ordinarily keep their eyes stabilized with respect only to the rotational components of their own movements. It was inferred that for an afoveate animal with laterally directed visual fields, monocular optokinetic stimulation in the u→c direction generates information sufficient by itself to determine unambiguously the direction of the appropriate stabilizing optomotor responses, whereas information generated by monocular stimulation in the opposite (c→u) direction may be inadequate—unless supplemented by other inputs—to specify the appropriate response. This follows from the fact that stimulation in the c→u direction normally is linked not only with rotation away from the side of the stimulated eye, but also (quite apart from rotation) with forward locomotion. Stimulation in the u→c direction, on the other hand, will indicate that the animal is turning toward the stimulated eye, regardless of whether the turning is or is not combined with forward locomotion. It was therefore postulated that optomotor unidirectionality will be a usual correlate of an afoveate visual organization, and that bidirectionality will be confined in the main to the foveate animals (*12*). The purpose of our study was to test this prediction by observations on a variety of animals having completely crossed visual pathways.

Table 1. Retinal and optomotor response characteristics of 4 mammalian and 19 reptilian species. At least two individuals were tested for each species (except woodchuck). A, afoveate; F, foveate; U, unidirectional; B, bidirectional; H and E, head and eye, respectively.

| Animal | Retinal type | Response to monocular stimulation in direction | | Re-sponse type | Main motor response by |
|---|---|---|---|---|---|
| | | u→c | c→u | | |
| *Mammals (lagomorphs and rodents)* | | | | | |
| Rabbit (*Oryctolagus cuniculus*) | Rod:A | 3 | 0 | U | H |
| Guinea pig (*Cavia porcellus*) | Rod:A | 3 | 0 | U | H |
| Prairie dog (*Cynomys ludovicianus*) | Cone:A | 4 | 0 | U | H |
| Woodchuck (*Marmota monax*)† | Cone:A | 0 | 0 | | E |
| *Reptiles (lizards and crocodilians)* | | | | | |
| African chameleon (*Chameleo melleri*)‡ | Cone:F | 6 | 6 | B | E + H |
| Blue-tongued skink (*Tiliqua scincoides*) | Cone:F | 4 | 3 | B | H |
| Horned toad (*Phrvnosoma cornutum*) | Cone:F | 5 | 5 | B | H + E |
| Common iguana (*Iguana iguana*) | Cone:F | 6 | 6 | B | H + E |
| Cuban anole (*Anolis equestris*) | Cone:F | 6 | 6 | B | E |
| Desert iguana (*Dipsosaurus dorsalis*) | Cone:F | 5 | 5 | B | H |
| Eastern collared lizard (*Crotaphytus collaris collaris*) | Cone:F | 5 | 4§ | B | H |
| Rhinoceros iguana (*Cyclura cornuta*) | Cone:F | 4 | 1 | U | E |
| Hardwicke's Dabb lizard (*Uromastix hardwickii*) | Cone:F | 5 | 5 | B | H + E |
| Australian water dragon (*Physignathus lesueuri*) | Cone:F | 5 | 4 | B | E |
| Asian water dragon (*Physignathus cochinchinensis*) | Cone:F | 4 | 1 | U | E |
| Girdle-tailed lizard (*Cordylus giganteus*) | Cone:F | 5 | 4§ | B | H |
| Gila monster (*Heloderma suspectum*) | Rod:A | 3 | 0 | U | H + E |
| Beaded lizard (*Heloderma horridum*) | Rod:A | 3 | 0 | U | H |
| Leopard gecko (*Eublepharus macularus*) | Rod:A | 5 | 0 | U | H |
| Day gecko (*Phelsuma madagascariensis*) | Cone:F | 6 | 5§ | B | H + E |
| Indian gavial (*Gavialis gangeticus*) | Rod:A | 3 | 0 | U | H |
| Black caiman (*Caiman c. melanosuchus*) | Rod:A | 2 | 0 | U | H + E |
| South American caiman (*Caiman crocodilus*) | Rod:A | 0 | 0 | | ¶ |

† Only one individual of this species tested; excellent OKN (exclusively ocular) during binocular stimulation; no response to monocular stimulation; repetition of binocular stimulation again revealed excellent OKN. ‡ Results reported previously (*13*). § This response elicited only after some delay; little or no response seen at the start of optokinetic stimulation, but good optomotor response (mainly or entirely head nystagmus) obtained after stimulation had continued 15 or more seconds. ¶ No true nystagmus seen; repeated testing elicited no consistent response.

Apparatus consisted of a vertically oriented cylindrical screen (*13*), 61 cm high and 76 cm in diameter, that could be turned in either direction at speeds up to 10 rev/min (60° per second) by an electric motor. A vertical pattern of alternating black and white 2.5-cm stripes covered the screen's inner surface. The only illumination was a 100-watt bulb suspended 90 cm above the top of the cylinder (lower levels of illumination were used during tests of certain nocturnal species). The animal was free to move around on the stationary platform which closed the lower end of the cylinder. Observation was from above through a transparent plexiglass cover.

The test group consisted of 4 afoveate species of mammals; 19 nocturnal and diurnal, foveate and afoveate species of reptiles (lizards and crocodilians); and 17 species of birds. The tests were designed to determine whether a clear optomotor response occurred in each of the two directions of cylinder rotation, under each of three visual conditions (vision with both eyes, with right eye only, and with left eye only). A stimulus speed range of 5 to 7 rev/min (30° to 42° per second) proved most satisfactory for this purpose, although lower and higher speeds were used at times. Each animal was first exposed to binocular optokinetic stimulation as a baseline for comparison with effects of subsequent monocular stimulation. For monocular stimulation a double thickness of black masking tape was placed over the closed eye. The initial direction of monocular stimulation was varied randomly, so that either direction (u→c or c→u) might come first. Two or more individuals of a given reptilian species were each tested under the six conditions; then the whole test procedure was repeated on the same day after a 15-minute rest period. For each reptilian species this procedure was repeated at least once at a later date.

Data were obtained by direct visual observation of each animal's movement under the different conditions. Verbal descriptions of behavior were recorded and supplemented by numerical ratings based on an arbitrary scale extending from 0 to 6: a rating of 5 or 6 was recorded for a vigorous optomotor response in the form of good OKN, strong head nystagmus, or consistent tracking of the stimulus pattern by locomotion; a rating of 3 or 4 indicated a less vigorous but still clear-cut and fairly consistent response; a score of 1 or 2 indicated that some optomotor reaction was obtained but was weak or inconstant; 0 meant no response. The species was classed as unidirectional if the average score for responses to c→u stimulation differed from that for response to u→c stimulation by more than 2 score units. Otherwise, the species was classed as bidirectional. Two to four observers witnessed each test. Eye, head, and body movements were generally easily observable, and agreement between observer ratings was usually close.

Guinea pigs and rabbits showed a unidirectional response to monocular OKN stimulation. This is consistent with earlier reports. Prairie dogs (afoveate, pure cone retina) also showed a unidirectional response, as predicted (Table 1).

More than half of the reptilian species were bidirectional in their responses to monocular optomotor testing, showing that degree of decussation of visual pathways cannot be decisive (Table 1). When these data are examined for relationship of response type to retinal type, it is seen that all the animals consistently exhibiting bidirectional responses were foveate, and all but two of the animals exhibiting unidirectional responses were afoveate.

Tests performed on 17 species of birds (one individual of each) showed optomotor bidirectionality in every instance (*14*). Birds have excellent vision; most have cone-rich retinas with an area centralis and single or double foveae, except for ground feeders and domesticated species, which are generally considered afoveate (*11*). On the basis of available information (*11*), we suspect that all our species are foveate.

These findings are almost entirely in accord with prediction. In the sample of reptiles all the afoveate species were nocturnal, and all foveate species were diurnal, suggesting that some other aspect of adaptation to diurnal or nocturnal conditions might provide an anatomic criterion as effective as presence or absence of a fovea for predicting bidirectionality or unidirectionality. However, the mammalian and avian data tend to support the special relevance of the fovea in two ways: The first is that the prairie dog (Table 1), domesticated pigeon (*9*) and chicken (*10*), although diurnal, gave unidirectional optomotor responses, and these forms differ from the previously tested diurnal mammals and most of the diurnal birds in that they are afoveate (*11*); the second is that the three species of owls all gave bidirectional optomotor responses, although two of the three were nocturnal species (*11*). Study of animals with pure rod foveae (*11, 15*) can further test this differentiation.

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15. For example, the gecko *Sphaerodactylus parkeri* [G. Underwood, *Nature* **167**, 183 (1951)].
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## Mongoose and Millipedes

Davis and I (*1*) have described the peculiar behavior whereby the African banded mongoose (*Mungos mungo*) hurls and smashes certain hard-shelled "pill" millipedes (order Glomerida) before eating them. The study was done with a caged mongoose at the New York Zoological Park and millipedes shipped to us from Africa. In several of the many letters received in response to our report, doubts about the validity of our findings were expressed because of the abnormal setting in which they were obtained. The following excerpt, taken from a book (*2*) which has only now come to my attention (*3*), attests to the occurrence of the behavior in nature.

> Mongooses . . . in captivity . . . eat almost anything, but in their wild state they live mainly on insects. A friend of mine recently told me a strange tale about one of these creatures. He's an old man, and he's more or less grown up in these wild stretches of Natal. He said that one morning when he was sitting quietly under a tree in the bush hoping to see some birds, he spotted a colony of mongooses nearby. Suddenly one of them climbed a short distance up a tree and knocked down a pill millipede. The mongoose jumped down after it, grabbed it between his front feet, and hurled it through his backlegs against the tree. The impact smashed the otherwise-impregnable ball, and before any of his friends could cheat him of his prey, he ate it.

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3. I thank Dr. R. F. Lawrence, Albany Museum, Grahamstown, South Africa, for alerting me to Mrs. Wager's book, and Mr. V. A. Wager for permission to reproduce the passage from his wife's book.

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