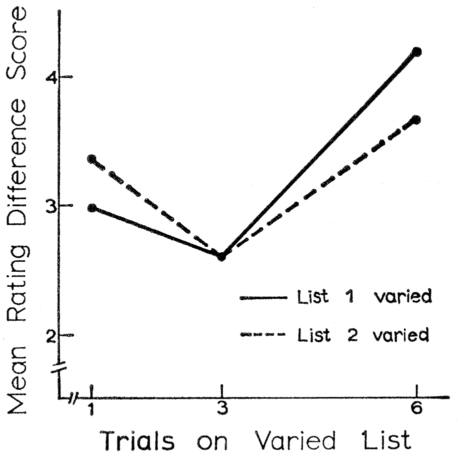

Fig. 1. The mean rating difference score for each group as a function of the number of trials on the varied list. The other list was always presented for three trials.

minutes after the final word in list 2 was shown, the 50 words from both lists were projected in a mixed order at an 8-second rate. Subjects were asked to indicate for each word their confidence that it had appeared on list 1 or list 2. They were assured that each test word had, in fact, been on one of the two lists. The subjects were instructed to use a six-point confidence rating scale in which ratings of "one," "two," and "three" corresponded to decreasing degrees of confidence in assigning a word to list 1, and ratings of "four," "five," and "six" corresponded to increasing degrees of confidence in assigning a word to list 2 (*7*). A rating of "one" meant that the subject was certain the item was from list 1, while a rating of "six" meant he was certain the item was from list 2.

A measure of each subject's differentiation was obtained by computing the difference between his mean ratings of the list 2 and list 1 words. The greater the difference score (the maximum is five) the better the differentiation between the lists. Figure 1 shows the mean rating difference score for each group in both studies as a function of the number of trials on the varied list (there were three trials on the constant list in each case). The 3-3 group serves as the mid-point for both functions. Both functions pass through a minimum at the 3-3 point. The results of a Kruskal-Wallis one-way analysis of variance show that each function differs significantly from chance ($H = 9.156$, $P < .02$, for second-list varied; $H = 21.535$, $P < .001$, for first-list varied). A more stringent test of whether the functions are significantly U-shaped was performed by comparing the differentiation score of the 3-3 group with the four adjacent points by the Mann-Whitney test. The only test that was not significant was of the 1-3 group versus the 3-3 group (for the 3-3 versus 3-1 comparison, $U = 121.5$, $P < .05$; for the 3-3 versus 1-3 test, $U = 168.5$, $P > .05$; for the 3-3 versus 6-3 test, $U = 49$, $P < .001$; for the 3-3 versus 3-6 test, $U = 97$, $P < .01$). The evidence is strong that differentiation is poorest when both lists are presented equally often. The superiority of the 6-3 over the 3-6 group, and of the 3-1 over the 1-3 group is not statistically significant in either case.

An alternative index of differentiation is the number of false identifications. False identifications were computed by regarding ratings of "one," "two," or "three" as equivalent to an identification of list 1, and ratings of "four," "five," and "six" as equivalent to a list 2 identification. Chance performance would produce a score of 25 on this measure. The mean number of false identifications for the 3-1, 3-3, and 3-6 groups are, in order, 6.90, 10.55, and 5.95. For the first-list varied groups, the comparable values are 8.60, 10.55, and 3.30. Statistical tests show the same pattern of outcomes as for the rating difference scores.

These results confirm the predictions of others that differentiation is a U-shaped function of trials on the varied list, with a minimum where both lists are of equal strength. They provide empirical support for the theoretical burden placed on differentiation in analyses of retroactive inhibition and transfer. Furthermore, our technique focuses on a phenomenon of memory which has been neglected by experimental psychologists to a considerable extent, namely the problem of the forgetting of context while retaining familiarity. A homely example is that of the teacher who has the experience of encountering on campus the familiar face of a former student without remembering in what class (or context) he knew the student. Shepard has shown that after one exposure to 540 words presented serially subjects can identify 88 percent of the words in a forced-choice recognition test (*8*). In our experiment, it is likely that the subjects were familiar with almost every word on the differentiation test, yet the 3-3 group achieved an identification score only 60 percent above chance. Apparently, the forgetting of context is a substantial phenomenon. Specification of the functional stimulus for the discrimination of list membership remains a task for research before the implications of these findings can be elucidated. However, our results indicate that the relative strengths of two response systems play an important role in their differentiation.

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Optomotor Responses by Echolocating Bats

Abstract. *Optomotor responses to moving stripes have been elicited from nine species of Microchiroptera. The minimum separable visual angle of two phyllostomids, under the experimental conditions, probably lies between 3.0 and 0.7 degrees; that of* Myotis lucifugus, *between 6.0 and 3.0 degrees. Four species indicate an ability to resolve stripes subtending 0.7 degree, the narrowest tested.*

Bats of the suborder Microchiroptera have a highly developed system for acoustic orientation, but little is known concerning their visual capabilities. All-rod retinas, lacking the mammillations characteristic of the Megachiroptera, have been reported in 16 species studied histologically (*1*). There is behavioral evidence, consisting largely of conditioned responses, indicating an ability by at least four species (*Myotis lucifugus, M. sodalis, Eptesicus fuscus,* and

Plecotus auritus) to distinguish between light and darkness (*2*); yet until now there has been no experimental evidence for the perception of moving forms or patterns.

The results of the following experiments suggest that at least some Microchiroptera have considerably better vision than has been generally supposed. Optomotor responses, movements of the head or body in response to optical stimulation, reported here for nine species of echolocating bats, constitute the first experimental evidence for possible pattern vision in these animals.

The bat to be tested was placed in a cylindrical, transparent, plastic chamber which prevented the echolocation of outside objects, including the test stripes (Fig. 1). This chamber was rigidly suspended at the center of a large aluminum cylinder which could be rotated smoothly by hand in either direction around the stationary chamber containing the bat.

The visual test stimulus presented to the bat consisted of alternating, vertical, black and white stripes of equal width marked on bristol board lining the cylinder wall. These stripes were illuminated by an incandescent bulb centered a short distance above the open top of the cylinder.

Cylinder liners were prepared with stripes subtending 30, 10, 5 (6 in the case of *Myotis lucifugus*), 3, and 0.7 degrees of arc, respectively, at the center of the chamber. A uniform gray liner (white in the case of *Saccopteryx bilineata*) was periodically inserted as a control. Stripe width could be quickly changed with minimum disturbance of the bat by inserting a different liner into the cylinder.

The cylinder was rotated only when the bat was motionless in the chamber. Rotation was continued at an approximately uniform speed of about 6 rev/min until either the animal moved or a set length of time had elapsed. The direction of rotation was varied semirandomly, each trial being separated by a stationary pause. Moderate variation in the speed of rotation did not appear to alter the behavior of the bat.

The bat was observed from above through a fixed grid at the top of the chamber, against which small movements could be more easily detected. Most species hung head downward but some (*Myotis, Desmodus,* and *Diaemus*) characteristically rested in a prone position on the chamber floor. Only movements of the head or body were recorded. Oculomotor responses, if they occurred, could not be detected as the eyes of the bat were seldom visible.

The optomotor response usually consisted of a turning of the head in the direction in which the stripes were moving. If the stripes continued to rotate, turning of the head was often followed by rotation of the entire body and finally by walking or flapping about inside the chamber. *Myotis lucifugus* and *Carollia perspicillata* responded by consistently turning in the direction opposite that in which the stripes were moving. There was a delay between the start of stripe rotation and any visible movement on the part of the bat. This delay ranged from 1 or 2 seconds to more than a minute, depending on the species being tested.

Extreme care was used to eliminate any possible extraneous visual, auditory, or other stimuli which might be associated with rotation of the cylinder. All experiments were performed in a quiet, dark room in which the stripe illumination was the only light source. There was no detectable audible or ultrasonic sound associated with cylinder rotation nor did motion of the cylinder cause any detectable movement or vibration of the independently mounted plastic chamber.

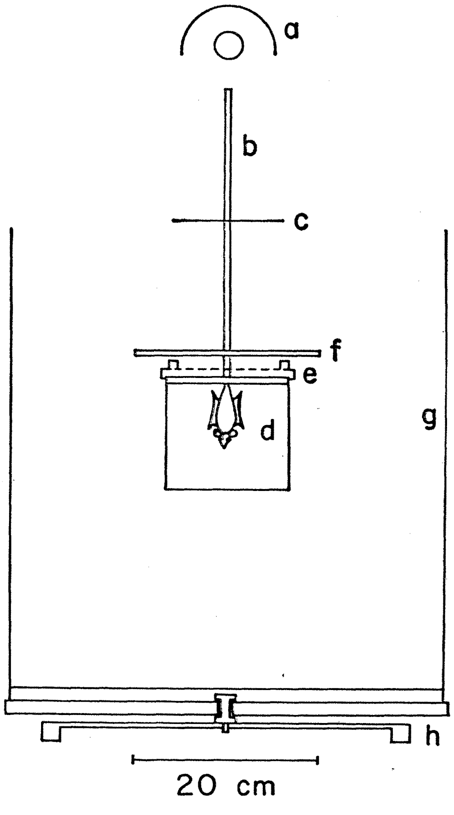

Fig. 1. Optomotor test apparatus: *a*, incandescent light source; *b*, support for central chamber; *c*, opaque horizontal disc shielding bat from direct illumination; *d*, transparent cylindrical plastic chamber containing artist's impression of a bat (a larger chamber was used for *Phyllostomus hastatus*); *e*, wire-mesh grid; *f*, clear plexiglass cover preventing echolocation through grid; *g*, aluminum cylinder with test stripes lining wall and with a uniform white floor; *h*, stand designed to allow smooth rotation of cylinder on bicycle wheel bearings.

Successful elicitation of optomotor responses depended upon the bat being in a proper psychophysiological state. It was therefore necessary to distinguish between absence of response because of lack of optical stimulation and absence because of a low degree of interest on the part of the animal. No series of control trials was considered valid unless it was immediately preceded and followed by trials eliciting clear responses to moving stripes, an indication of a consistently high interest level. Trials with narrow stripes which elicited no response were thus sometimes used as controls for wider stripes. In three species it was possible in this way to obtain estimates of the approximate minimum separable visual angle.

The data presented in Table 1 are for the individual bat of each species that yielded the most consistent data. In several cases additional animals were tested and responded similarly. In some cases optomotor responses could be elicited from only one of the few individuals tested. A number of species not included here were also tested but gave no optomotor responses.

The most important data obtained for each species are summarized as two rows in Table 1. The upper row indicates the narrowest stripe tested which elicited a clear optomotor response. The difference in the number of movements in each direction for trials in this row is significant at the 1-percent level according to adjusted chi-square tests of the null hypothesis. The lower row summarizes data obtained with a uniform gray (or white) control liner or with narrower stripes when they were available. Under these conditions, the direction of the bats' movements is not significantly correlated with the direction of the stripe rotation.

The differences between the upper and lower rows in the ratio of the number of trials on which the bat moved in either direction to the number on which it did not move is also highly significant, except in the case of *Diaemus youngi* where these ratios are

Table 1. Optomotor responses of echolocating bats.

Bat	Visual angle subtended by stripe (degrees)	Number of trials on which bat moved		Total No. of trials	Trials on which bat moved (% total)
		Same direction as stripes	Opposite direction to stripes		
		Emballonuridae			
Saccopteryx bilineata	5.0	46	0	47	(98)
	white	0	4	20	(20)
Saccopteryx leptura	0.7	34	1	38	(92)
	gray	1	1	15	(13)
		Phyllostomidae			
Phyllostomus hastatus	3.0	17	0	18	(94)
	0.7	0	0	> 8	(0)
Anoura geoffroyi	0.7	24	0	26	(92)
	gray	0	0	15	(0)
Carollia perspicillata	0.7	1	35	39	(92)
	gray	1	2	17	(18)
Artibeus jamaicensis	3.0	18	0	19	(95)
	0.7	0	0	> 8	(0)
		Desmodontidae			
Desmodus rotundus	0.7	24	3	29	(93)
	gray	3	2	15	(33)
Diaemus youngi	3.0	41	9	53	(94)
	gray	21	28	51	(96)
		Vespertilionidae			
Myotis lucifugus *	6.0	0	16	18	(89)
	3.0	14	12	47	(55)
Myotis lucifugus †	6.0	0	15	23	(65)
	3.0	3	4	29	(24)

* 7.5 Watts. † 100 Watts.

similar. This bat was characteristically more active in the chamber than were any of the other species studied.

During experiments with neotropical species (first three families in Table 1) the stripes were illuminated by a 100-watt, 120-volt bulb operated at 60 volts and positioned 20 cm above the top of the cylinder. The illumination provided at this voltage was near the minimum at which the experimenter could still clearly distinguish the outline of the bat's body against the white floor of the cylinder. Experiments with *Myotis lucifugus* were conducted at two levels of stripe illumination both of which gave similar results. One series of experiments employed a 7.5-watt bulb; the other, a 100-watt bulb. In both cases the bulbs were operated at their rated voltage of 120 volts and were positioned 40 cm above the top of the aluminum cylinder.

The data indicate that, under the above experimental conditions, the minimum separable visual angle of *Phyllostomus hastatus* and *Artibeus jamaicensis* probably lies between 3.0 and 0.7 degree, and that of *M. lucifugus*, between 6.0 and 3.0 degrees, as judged by optomotor responses. Four other species responded to 0.7 degree—the narrowest stripes available. At the time *Saccopteryx bilineata* was tested, stripes narrower than 5.0 degrees were not available. Consistent data for 0.7-degree stripes have not yet been obtained with *Diaemus youngi* because of its restless behavior in the chamber (*3*).

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3. The data reported here suggest that the visual capabilities of echolocating bats may vary significantly between species or higher taxa and be correlated with particular feeding habits, ecological niches, or behavior patterns. Bats of the genus *Saccopteryx* are insectivorous species which often feed in the daytime and roost on exposed surfaces of forest trees. *Phyllostomus hastatus* is a large omnivorous bat whose diet includes fruit, insects, and small vertebrates. *Anoura* is a nectar feeder; *Carollia* and *Artibeus* are frugivorous. The Desmodontidae, or true vampires, live solely on blood of birds and mammals. *Myotis lucifugus* is a common temperate-latitude insectivorous species. Investigations are now in progress in an attempt to elucidate the possible importance of vision as a sensory modality, along with echolocation, in the lives of Microchiroptera.
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Electroencephalographic Activation: Nonspecific Habituation by Verbal Stimuli

Abstract. *A decrease in the duration of the electroencephalographic activation response to a series of different words: emotional, "neutral," and scrambled occurred. The response to "neutral" words was consistently briefer than that to the other words. This result is evidence of a nonspecific habituation of activation, which implies that habituation to classes of stimuli can occur.*

In his discussion of the extinction of the orienting reflex, Sokolov utilizes the concept of a "nervous model" of the stimulus (*1*). The magnitude of the orienting response is assumed to be proportional to the difference between the brain representation of the present stimulus and the nervous model of prior stimuli.

The nervous model is described as a multidimensional memory trace representing simultaneously the intensity, quality, and temporal characteristics of the previous stimuli. If a new stimulus differs from prior ones by more than a just-noticeable difference, the orienting reflex is reinstated. The components of the orienting reflex follow the same rule. The duration of electroencephalographic (EEG) activation decreases while the latency of activation increases with repeated stimulation. After a change of stimulation, the duration of activation increases and latency decreases (*2*).

Sokolov also proposed that after repeated presentation of stimuli varying within a restricted range, the nervous model is generalized to match the range of stimuli. There is surprisingly little EEG experimental data relevant to this hypothesis. In an extensive review of the problem of arousal in the nervous system, Gray (*3*) notes that he did not know of any studies of the extent of stimulus generalization during the stages of generalized and localized EEG activation. The following experiment confirms Sokolov's hypothesis.

Various words (in capital letters) were flashed onto a screen in a controlled temporal relation with the EEG occipital alpha-activation cycle (*4*). Occurrence of alpha (8 to 13 cy/sec, $> 5 \mu v$) caused a relay to close ("on"). Nonoccurrence of alpha caused it to open ("off"). This relay controlled the stimulus function. When alpha occurred for 0.4 second, a syllable was