Finck, A. and C. F. Reed 1979. Behavioral response to whole-body vibration in the orb-weaver *Araneus sericatus* Clerck (Araneae: Araneidae). J. Arachnol., 7:139-147.

BEHAVIORAL RESPONSE TO WHOLE-BODY VIBRATION IN THE ORB-WEAVER *ARANEUS SERICATUS* CLERCK (ARANEAE: ARANEIDAE)

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ABSTRACT

Orb-weaving spiders of the species *Araneus sericatus* demonstrate a reflex among the first or second pair of legs in response to vibrational pulses delivered to the substrate. This response served as the dependent variable in determining the absolute threshold sensitivity to vibration. Sensitivity was best (smallest displacement amplitudes) in the region of 125 hertz. The reaction time of the response was inversely related to vibration intensity. The response occurred within 100 milliseconds for suprathreshold stimuli. This study confirms, by a behavioral method, the frequency response range of the orb-weaver as indicated in physiological research. Evidence is given which shows that *A. sericatus* can respond to acoustical stimuli at frequencies greater than about 300 hertz.

INTRODUCTION

The mechanical stimulation produced in the web by struggling prey may or may not provide distinctive signals for the orb-web spider. Impact and motion of prey seem to be the events which initiate the response; there appear to be no anticipatory movements stimulated by the wingbeat of approaching insects, although the effectiveness of sound as a stimulus has been established in several species of spider (Frings and Frings 1966, Walcott 1969). Moreover, the visual capacity of the orb-web spider is insufficient for the supposition that it plays any role in identifying the contents of the web.

There are several strategies in establishing the spider's mechanical sensitivity. One productive course is to measure the response of single neurons when legs are moved or vibrated (Finck unpublished, Walcott and Van der Kloot 1959) or when slit-organs are selectively stimulated (Barth 1967, Barth and Bohenberger 1978). It is probably, but not necessarily, the case that the mechanical sensitivity of the animal can be deduced from knowledge of the responses of individual nerve cells— assuming the sensory apparatus to have been accurately and completely identified. Not all investigators have been comfortable with that assumption and have attempted to assess sensitivity *in situ*, that is, with the spider exposed to nearfield and farfield vibration while in its web (Frings and Frings 1966, Walcott 1963). However, as Frings and Frings have pointed out (1966), it is difficult to determine the precise characteristics of the stimulus as received by the spider at the hub. If vibration is applied to the catching zone of the web, for instance, the signals are attenuated and altered as they travel across the intervening network of threads.

We have chosen a third approach, in which the dependent variable is behavioral rather than electrophysiological, and in which vibration is applied to a solid substrate on which the animal is resting. Some of the limitations of the other approaches are avoided by this procedure, but on the other hand certain limitations of this technique have also to be borne in mind; they will be discussed in evaluating the results of the study.

METHOD

Vibratory stimuli were employed to elicit a motor response in female spiders of the species *Araneus sericatus* Clerck. We refer to this response as the vibratory motor response (VMR). It is a twitch of the first or second pair of legs. The movement is of brief duration and is not necessarily visible to the unaided eye, although it may be followed by gross movements as the animal retreats or readjusts its position.

In employing a behavioral measure, it is of course necessary not only that the stimulus be precisely specified, but that phenomena such as habituation be controlled. The motor response involved in the spider's dropping from the web, which the Peckhams (1887) and later Savory (1934) attempted to use in assessing vibratory sensitivity of orb-weavers, is complicated by progressive waning of the response with repeated application of the stimulus. A similar problem confronted Frings and Frings (1966) in using the spider's spasmodic extension of the first legs as an index of response to airborne vibration. The effects of habituation may be avoided by appropriate temporal spacing of trials. In the case of the VMR, we were able to establish by pre-testing that habituation could be avoided by spacing stimulation trials by at least 60 seconds.

The system for detecting and recording the VMR is shown in Fig. 1. The spider subject was placed in a translucent chamber mounted directly to a Pye-Ling V47 vibrator. A Sony video camera mounted on the side-arm of a Zeiss operating microscope delivered an image of approximately 17 X magnification to a TV monitor. Illumination was provided by a light source within the microscope. A photocell positioned over the image of the legs on the TV monitor detected minute movements of the legs. The photocell voltages were filtered (to remove the effects of the TV raster), amplified and permanently recorded on FM magnetic tape. A second tape channel recorded a timing pulse which marked the onset of the stimulus.

The stimulus consisted of a 300 msec pulse with a rise-decay time of 25 msec (thus voiding onset-offset transients). Stimulus amplitudes were controlled by attenuators matched to the impedance of the vibrator. Stimulus vibratory frequencies between 50 and 600 Hertz were delivered to the vibrator. Careful calibration was accomplished by the use of an accelerometer attached to the spider chamber and by direct, optical measurement. The vibration amplitude is reported in this study in decibels (dB) relative to a displacement of one micron. Thus, 0 dB=1 micron root-mean-square (rms), -10 dB= 0.316 micron rms and -20 dB= 0.1 micron rms. (The root-mean-square, an equivalent to the standard deviation of the peak displacement of a sine wave, has traditionally been employed to specify the amplitude of stimuli in studies of vibration).

The Vibratory Motor Response and Threshold Criteria.—The VMR served as the dependent variable for estimating the vibratory responsiveness of the spider. Fig. 2 shows the VMR for two animals at six different displacement levels and two frequencies. The response is clearly distinguishable from baseline variations. The duration of the response varies between 100 and 200 msec (near the baseline). At vibrational intensities near threshold the VMR is often of smaller amplitude than at substantial suprathreshold levels, but the relationship between intensity and response amplitude is not sufficiently consistent to permit us to employ the vigor of the response as an indicator of sensitivity. On the other hand, the examples of the response shown in Fig. 2 demonstrate that response latency is related to the stimulus: reaction time decreases with increased vibrator displacement. On the TV monitor the VMR is seen as a minute lateral deflection of the first or second leg. The movement is probably similar to the reflex reported by Seyfarth (1978) in *Cupeinnius salei* Keys. Seyfarth found that it could be elicited by application of sinusoidal displacements to the tarsus, but he did not report the stimulus-response latencies.

The vibration threshold at a particular frequency was defined as that intensity which just evoked a VMR. Our procedure was to deliver stimuli in ascending steps according to a Method of Limits. The first stimulus was presented well below the estimated threshold and increased in amplitude by five decibel steps until the VMR appeared. The response was confirmed by increasing the amplitude of the vibrator another five dB. In order to exclude responses not contingent upon the stimulus, a time-window of 2.5 secs was set. Leg movements which occured with latencies exceeding this interval were not considered responses. Sometimes a spontaneous movement occurred just before the delivery of a stimulus: those trials were excluded.

RESULTS

The results are based upon the responses of 22 spiders given a total of 823 trials at 14 different vibration frequencies. The response region for the species was calculated by tabulating the attenuation values obtained at threshold. Having determined the proportion of responses from all the animals at a given level, we converted the attenuation levels (relative dB) into displacement according to our calibration of the Pye-Ling vibrator.

Figure 3 shows the thresholds for the total sample of animals. The ordinate is given in decibels re: 1 micron rms. Thus zero dB represents a 1 micron displacement and + 20 dB a 10 micron displacement. Vibration frequency (in Hz) appears on the abscissa. The two curves in the figure represent the median threshold value (half of the animals required greater, half smaller displacement to produce the threshold response) and the 75th percentile (75 percent of the animals required greater displacement to reach threshold and 25 percent required smaller).

The median (50 percent) results (closed circles) show an increasing sensitivity between 50 and 125 Hz and a rapid decrease for frequencies exceeding 125 Hz. The 75th percentile curve (open circles) demonstrates an overall lower absolute threshold because it employs a more liberal criterion for definition of threshold. Together these results indicate that the best amplitude sensitivity for the animals is between 125 and 150 Hz.

An inevitable feature of a vibrator, especially when it operates at a substantial level, is to produce sound. In assessing sensitivity to movement of the substrate, it is necessary to exclude sound as a possible stimulus. Figure 3 contains, on the right, data points not joined to their appropriate (median or 75th percentile) curves. They represent thresholds for frequency locations at which the spider was apparently responding to sound rather than to direct ivibration. This condition was established by retesting 5 of the 22 animals while exposed to a continuous acoustic noise. Specifically, a 90 dB (re: 0.0002 microbar) white noise was delivered to the spider chamber while vibration thresholds were repeated in the usual manner. This acoustic masking noise had no observable effect on thresholds taken below 300 Hz, but stimuli above 300 Hz, which had previously been effective in eliciting the response, did not do so in the presence of the masker.

Figure 4 shows response latency (reaction time) of the VMR as a function of vibration intensity. The ordinate represents time (in msec) from the onset of the stimulus to the peak amplitude of the VMR (see Fig. 2). The abscissa represents the displacement of the stimulus in terms of attenuation. For example, -25 dB is a stimulus displacement 0.56 times smaller than zero dB, and -10dB is a displacement 0.316 of the displacement at zero dB. These data demonstrate that when the intensity of the stimulus is increased the reaction time of the VMR decreases. The response latency curves are non-linear and they tend toward an asymptote at the higher stimulus intensities (i.e. the smaller attenuation values). The dynamic range (intensity sensitivity) is seen to be at least 15 dB for most of the spiders. One animal shows a very restricted range of sensitivity, about 5 dB. The reaction times of the VMR were measured to the peak of the response with some of the shortest latencies occurring in the region of 100-200 msec. Of course, reaction times measured from the very first indication of a response would have yielded lower values; in several of the animals such latencies would have been much less than 100 msec.

DISCUSSION AND CONCLUSIONS

Our results demonstrate that the sensitivity of *A. sericatus* to substrate vibration ranges from at least 50 Hz to about 200 Hz. In the region of 125 Hz the threshold amplitude is near 10 microns displacement (75th percentile curve). Electrophysiological research has described lower displacement thresholds.

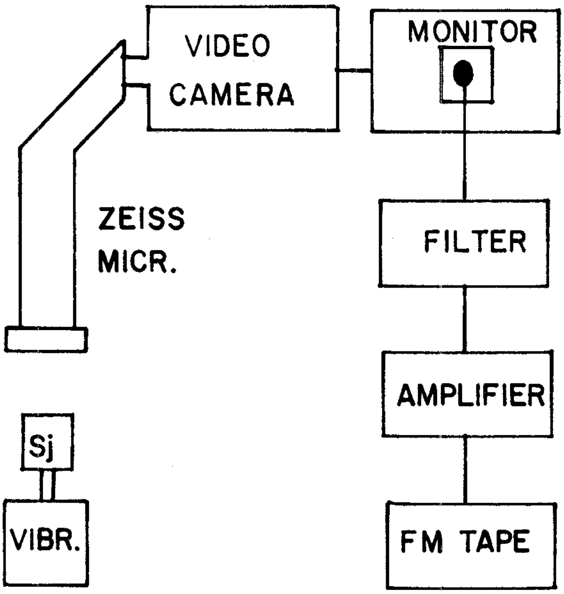

Fig. 1.–Schematic diagram of the recording system. The spider chamber (S_j) is mounted directly on the vibrator (VIBR). A photocell (black circle), positioned at an aperture in an opaque shield is placed on the enlarged video image of the leg. Small movements of the legs change the relative intensity of the light, producing changed photocell voltages which are filtered, amplified and recorded.

Walcott and Van der Kloot (1959) studied threshold sensitivity in *Achaearanea tepidariorum* with electrophysiological techniques. They reported thresholds of about 0.025 microns at 2000 Hz. Finck (1972) also employed an electrophysiological measure for the determination of sensitivity in *Araneus diadematus*. His results indicated that frequency sensitivity was best in the region of 90-150 Hz. This is a frequency region which corresponds to the behavioral sensitivity of *A. sericatus* (present study). Finck (unpublished results) has also recorded from single neural units in the leg ganglia of *A. sericatus*; these unit thresholds indicate a best frequency region of 90-125 Hz with occasional thresholds as low as 0.22 microns but with most requiring at least 30 microns displacement.

The behavioral thresholds reported in the present study are of the same order of sensitivity as the majority of single unit thresholds in the same species. However, as indicated above, a few single neurons may demonstrate considerably smaller displacement sensitivities.

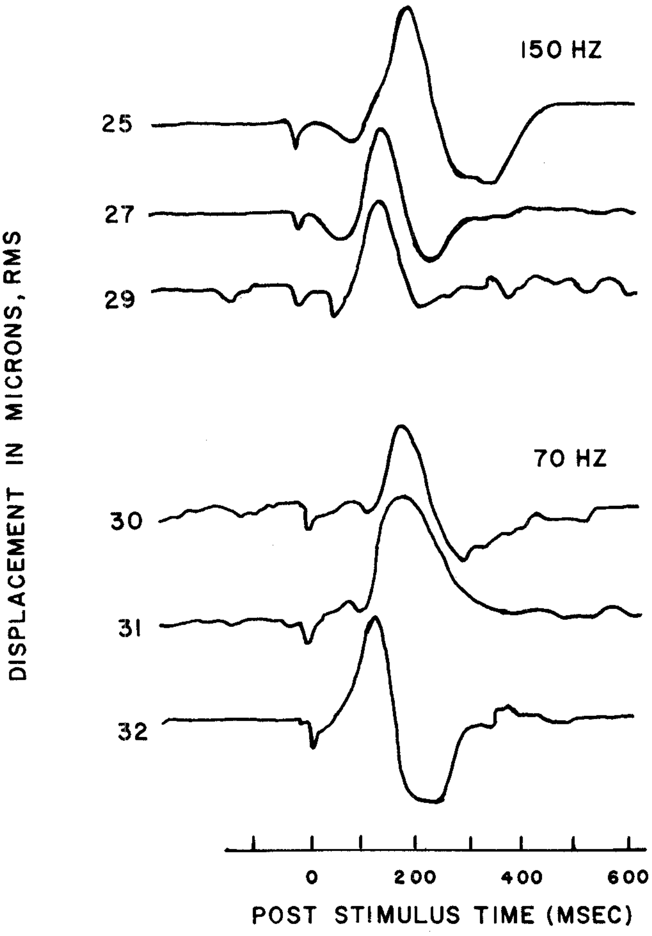

Fig. 2.–Vibratory motor response (VMR) at increasing stimulus amplitudes at two frequencies. The ordinate represents vibrator displacement in microns for stimulus frequencies of 70 and 150 hertz. The tracings record changes in position of a leg following the onset of a 300 msec pulse at time zero on the abscissa.

In evaluating this finding, we may consider the relative roles of acoustic and substrate vibration. A spider's response to sound has been observed and studied by several investigators (Barth 1967, Frings and Frings 1966, Peckham and Peckham 1887, Walcott and Van der Kloot 1959). We were able to separate the direct-vibration component from the sound-induced component of the sensitivity curve by introducing a masking noise. This masking noise obviated the effect of stimulus frequencies above 300 Hz. That is, in the presence of the masker, vibration of the substrate for these frequencies was ineffective in producing responses. Thus sensitivity to direct-substrate vibration does not appear to extend above 300 Hz. Consequently it is possible that the exquisite sensitivity of the spider to higher frequencies may be due to sound in the near field.

It may well be the case that the lyriform organ transduces both direct vibration and acoustic energy. Some evidence for that possibility is given in the research of Barth (1967), who demonstrated that a single slit-sense organ in *Cupiennius salei* could respond to sound stimuli. Walcott and Van der Kloot (1959) also demonstrated that the excised leg of *A. tepidariorum* was sensitive to both sound and vibration. Our results indicate that

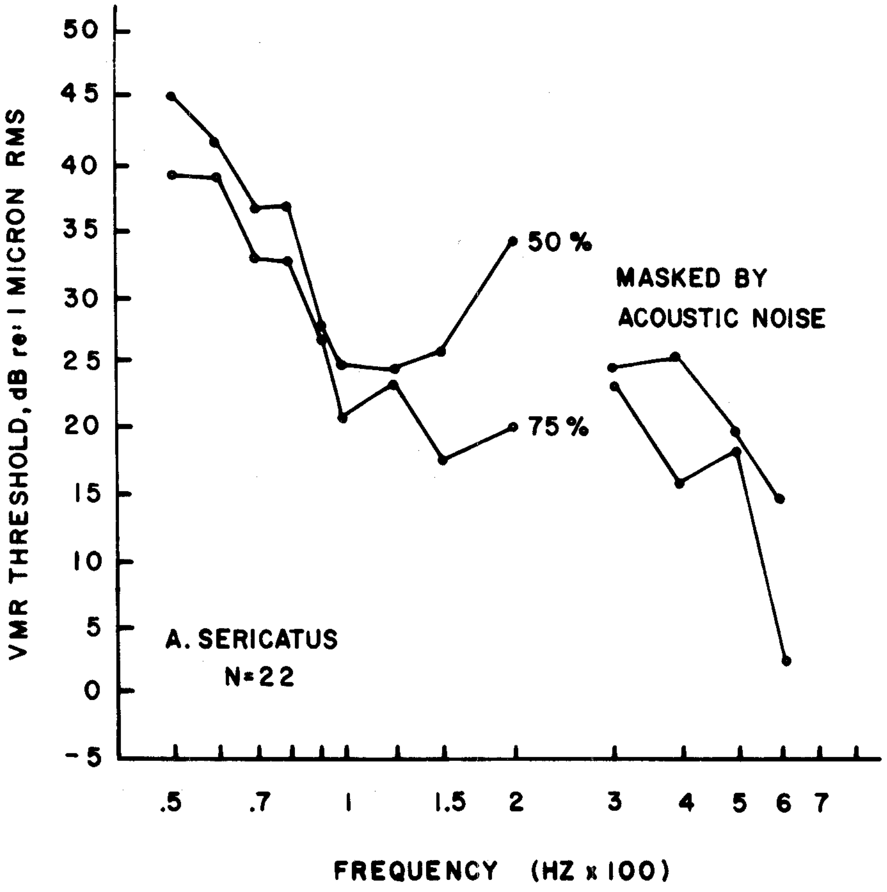

Fig. 3.–Vibration threshold as a function of frequency. The ordinate is stimulus displacement in dB where zero dB equals 1 micron. Frequencies "masked by acoustic noise" show thresholds obtained only in the absence of a 90 dB acoustic noise.

in the acoustic region of *A. sericatus* (300 Hz and higher) threshold displacement decreases rapidly (see Fig. 3, region marked "Masked by Acoustic Noise"). This finding is precisely what would be expected for sound waves in the near field: an inverse relationship between displacement amplitude and frequency. Therefore for *A. sericatus* the region of 300 Hz appears to be a kind of demarcation point above which acoustic pressure alone is the salient stimulus dimension.

It is still possible only to speculate on the relationship between vibration sensitivity in the orb-weaving spider and the production of vibro-acoustic stimulation by insects captured in the web. Little is known about the web as a transmission link between the source of vibration and the spider, although Walcott (1963) has shown that single strands of spider silk (taken from *A. tepidariorum*) can transmit vibrations from about 50 to 2000 Hz. He also found that the attenuation of vibratory displacement is only about 1.2 to 1.5 dB per centimeter of thread, a finding which would make the thread an efficient substrate for the transmission of vibrations to the spider. However, there may be some danger in generalizing this observation to vibratory characteristics of the whole web,

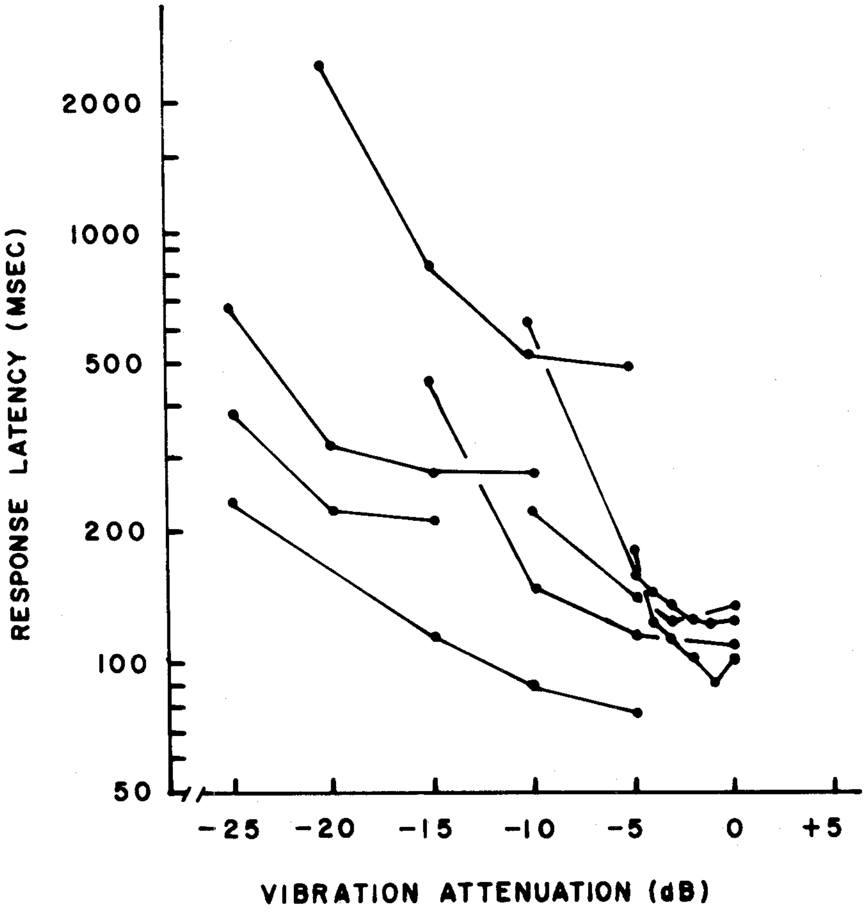

Fig. 4.–Latency of the VMR as a function of vibration amplitude (8 animals). Latency is measured from the onset of the stimulus to the peak amplitude of the response. The abscissa shows attenuation (relative vibration amplitude) in decibels.

which is a complex, interconnected structure, and which can vary in its parts in tension, thickness of thread, and mode of attachment, to name only a few variables.

Further, there is to our knowledge no report on the generation of web vibration as opposed to acoustic pressure by insects ensnared in the web. Walcott (1969) did report on the honey bee and the house fly as acoustic sources in the near-field when snared. In these observations the main acoustic energy peaks were located at about 700 Hz for the house fly and at two peaks of 500 and 2000 Hz for the honey bee. These represent acoustic frequencies well above the vibratory sensitivity of *A. sericatus* as found in the present study and for *A. diadematus* (Finck 1972). Nor does it appear that the web acts to convert pressure waves at acoustic frequencies into web motion and thus vibration to which the spider could respond. Finck, Stewart and Reed (1975) studied the resonant characteristics of the web of *Araneus diadematus* Cl. in a sound field. Their results showed that even in relatively intense sound fields (+90 dB re: 0.0002 microbar) web movement peaked near 25 Hz with virtually no movement for other frequencies between 20 and 20,000 Hz. The orb web of that species, and probably of other species with webs of similar geometry, cannot serve as an acoustic detector for the approach of flying insects with wing beats exceeding 25 Hz. To the extent that *A. sericatus* employs only the direct vibratory system described here, it is largely isolated from distant sound sources. At least as a detector of direct vibration, it is restricted to rather low frequencies.

Finally, some comments must be made on the utility of the present procedure. While it furnishes specifiable, direct stimulation, and avoids some complications of testing the animal in the web, it is well to keep limitations in mind. The legs and body are directly vibrated, but are not in the posture characteristic of the spider hanging in the web. It is very possible that the posture represents an optimal positioning of receptors and accessory structures, or may provide ready adjustment in order to enhance sensitivity, for instance by extending the legs. Walcott and Van der Kloot (1959) had reported that, in *A. tepidariorum*, frequency response could be altered by changing the position of a leg. Finck (unpublished data) was unable to confirm that result for *A. sericatus* but did find that thresholds at a given frequency could be improved by altering the position of the leg. It may be the case that the spider can, by positioning its legs, exert control over the sensory input; this possibility remains to be demonstrated.

ACKNOWLEDGEMENTS

This work was supported by a grant from the Faculty Research and Study Leaves Committee of Temple University.

LITERATURE CITED

Barth, F. G. 1967. Ein einzelnes Spaltsinnesorgan auf dem Spinnentarsus: seine Erregung in Abhangigkeit von den Parametern des Lustschallreizes. A. vergl. Physiol., 55: 407-499.

Barth, F. G. and J. Bohnenberger. 1978. Lyriform Slit Sense Organ: Thresholds and Stimulus Amplitude Ranges in a Multi-Unit Mechanoreceptor. J. comp. Physiol., 125: 37-43.

Finck, A. 1972. Vibration Sensitivity in an Orb-Weaver. Am. Zoologist, 12: 539-543.

Finck, A., G. M. Stewart and C. F. Reed. 1975. The orb-web as an acoustic detector. J. Acoust. Soc. Am., 57: 753-754. Frings, H. and M. Frings. 1966. Reactions of Orb-Weaving Spiders to Airborne Sounds. Ecology, 47: 578-588.

Peckham, G. W. and E. G. Peckham. 1887. Some observations on the mental power of spiders. J. Morphol. Physiol., 1: 383-419.

Savory, T. H. 1934. Experiments on the tropisms of spiders. Queksett Microscop. Club, 53:13-24.

Seyfarth, E-A. 1978. Lyriform slit sense organs and muscle reflexes in the spider leg. J. comp. Physiol., 125: 45-57.

Walcott, C. and W. G. Van der Kloot. 1959. The Physiology of the spider vibration receptor. J. Exptl. Zool., 141: 191-244.

Walcott, C. 1963. The effect of the web on vibration sensitivity in the spider *Achaearanea Tepidariorum* (Koch). J. Exp. Biol., 40: 595-611. oWalcott, C. 1969. A Spider[s Vibration Receptor: Its Anatomy and Physiology. Am. Zoologist, 9: 133-144.