THE EFFECT OF THE WEB ON VIBRATION SENSITIVITY IN THE SPIDER, *ACHAEARANEA TEPIDARIORUM* (KOCH)*

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The common house spider, *Achaearanea tepidariorum*, has a sensitive vibration receptor in each of its eight legs. The receptor has been shown to respond to air-borne sound as well as to direct vibration (Walcott & Van der Kloot, 1959). But for a spider on its web a more usual source of information about the outside world comes from vibrations of the web strands themselves. What is the response of the receptor to the vibrations of the web? Liesenfeld (1956, 1961) has described some of the properties of spider webs and recorded the electrical response of the vibration receptors of a variety of species of spiders to vibrations of the substrate. Nowhere, however, can one find information on how vibrations of the web are translated by the spider's vibration receptor into electrical impulses in the sensory nerve.

One of the striking characteristics of the spider's vibration receptor is its dramatic variation in sensitivity to closely adjacent frequencies of air-borne sound. It appears that the ten receptor units of which the sense organ is composed are tuned. The sharpness of this tuning is such that the threshold of the preparation may vary by as much as 1 db. as the frequency is changed 1 cyc./sec. from 250 to 251 cyc./sec. When the tip of the leg was cemented to a crystal phonograph pick-up cartridge instead of being left free to vibrate in response to air-borne sound, the variation in threshold sensitivity to different frequencies disappeared. But a spider responding to vibrations of the strands of its web must be undergoing a direct vibration of its legs. Are all the characteristics of the sense organ's response to air-borne sound, the peaks in the threshold and the frequency discrimination, just an artifact of the experimental arrangement or do they play a significant role in the life of the spider as an integral property of its vibration receptor?

This paper will examine the role of the web in the spider's sensitivity to vibration and to air-borne sound. Included in this report are data on the transmission of vibration by single strands of spider silk and on the effect of these web strands upon the sensitivity, tuning and frequency discrimination of the receptor. In addition, the sense organ's response to web-borne vibrations is compared with its response to air-borne sound. These electrophysiological investigations have raised several questions about the spider's use of the information its receptor provides. For this reason, data on the frequencies of vibration and sound generated by insects snared in spider webs and on the responses of spiders to these vibrations are also included.

Animals

Spiders were collected from local barns and during the winter months from the elephant house at the local zoo. They were stored in 1 oz. paper cups and fed a weekly diet of a mealworm and a drop of water. Survival of the spiders was poor and no successful moulting occurred if the mealworms were fed a diet of standard mealworm bran. Feeding the spiders with mealworms reared on a diet of Kellogg's or Post's 40% Bran Flakes resulted in excellent survival and rapid growth.

Web transmission

For the measurement of the transmission of vibration by the web two crystal phonograph pick-up cartridges equipped with 1 cm. long glass probes were mounted side by side. The output of an audio oscillator was connected to one and the output of the other crystal was amplified and then connected to a voltmeter. A spider was anaesthetized with CO_2 and the tip of its spinnerets was touched to one of the needles. The animal was then moved towards the other cartridge and its silk wrapped around the glass probe. The tension of the silk strand connecting the two cartridges was that produced by the spider's spinnerets and was, therefore, probably close to that found in the usual web. Throughout this paper this will be referred to as 'normal' tension. The tension was increased by moving the two cartridges apart.

Measurements of transmission at various frequencies were begun with the crystals close together connected by a short strand of web. A longer strand of web was then substituted and the transmission measurements were repeated. In order to minimize the effect of the non-uniform frequency response of the crystals, the difference in transmission between the various lengths of web strands is reported.

Electrophysiology

Either the isolated spider leg or the entire spider was mounted on a Lucite holder. In this holder the spider is firmly cemented to a Lucite block and one of the front legs is inserted through a hole in the block. Midway through the hole in the block the leg is pierced by a fine tungsten microelectrode. The tip of the leg protrudes free beyond the far side of this solid block. The indifferent electrode is a silver–silver chloride electrode placed in a pool of Ringer's solution near the spider's cephalothorax. With this arrangement there is no danger of the electrodes moving and of confusing the vibrations of the electrodes with those of the web strand to which the spider leg is attached. With the tungsten electrode thrust through the cuticle of the leg near the lyriform organ at the tarsal-metatarsal joint, and with an indifferent electrode placed at the base of the leg, and if the preparation is shielded from air currents, the only action potentials that are recorded are those from the lyriform organ.

The tarsal claws at the tip of the rigidly held leg were attached to a strand of spider silk. In most cases this was a strand of silk about 20 cm. long stretched between either a magnetic disk recording head (Sure Model M 41) or a crystal phonograph pick-up cartridge and a rigid support. The vibrator could be arranged to vibrate the web strand either at right angles to, or parallel to, the long axis of the web strand. Generally about 10–15 cm. of silk intervened between the leg tip and the vibrator. By changing

the position of the supports both the tension of the web strand and the tension between the web and the leg could be varied independently.

The experiments were conducted in a variety of enclosures. Initially an Audiometric Test Chamber type 401 was used, but on finding some standing waves and a relatively high noise level, operations were moved to the anechoic chamber in the Harvard Cruft Laboratory. Since results obtained in the anechoic chamber were in every way comparable to those found in the small test room, further experiments were performed in the smaller, more convenient enclosure.
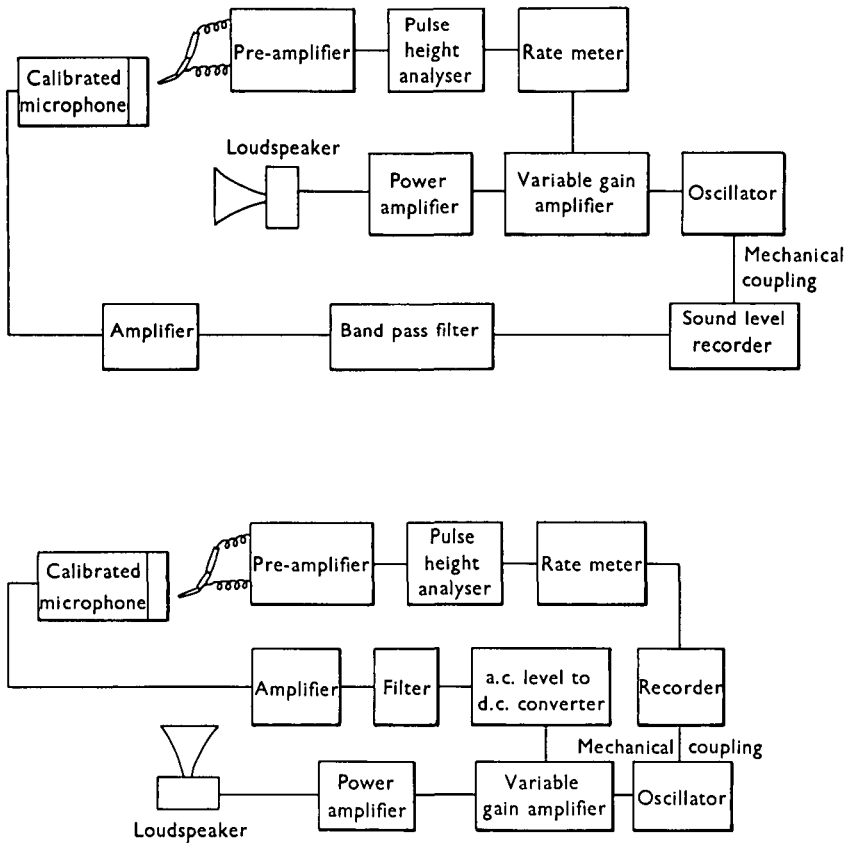

Fig. 1. A block diagram of the equipment used to measure automatically the threshold sensitivity of the spider's leg to sound of various frequencies. The top diagram shows the equipment arranged to maintain a constant number of action potentials. In this case the sound pressure necessary to maintain a given rate is recorded. The lower diagram shows the same equipment used to maintain a constant sound pressure at the leg and to record the rate of action potentials elicited.

The electronic equipment for amplifying the nerve impulses and for generating and measuring sound and vibration have been described previously (Walcott & Van der Kloot, 1959). One change from the previous technique is a method of automatically and rapidly measuring the 'threshold' sensitivity of the leg to a wide range of frequencies. This technique uses the rate of impulses appearing in the sensory nerve to control the loudness of the stimulating sound. By this method, a 'servo-loop'

is formed; the sound level is automatically regulated to that intensity which elicits a predetermined rate of action potentials from the leg. Thus, at any given moment, the sound level is proportional to the threshold of the sense organ at that frequency.

Since this technique might be helpful in other situations a brief description follows:

A block diagram of the equipment is given in Fig. 1. The action potentials from the spider leg are amplified by a preamplifier, the output of which is fed to a pulse-height analyser (Littauer & Walcott, 1959). A frequency meter (Hewlet-Packard 500B) is connected to the pulse-height analyser in such a fashion that one can choose between measuring the total activity of the leg nerve or the activity of one of the five arbitrarily selected groups of nerve fibres. The rate meter develops a voltage which is proportional to the rate of action potentials. This d.c. control voltage is used to vary the gain of an amplifier interposed between an audio-frequency oscillator and the power amplifier which drives the loudspeaker. Thus an increase in the number of action potentials reduces the gain of the amplifier and decreases the loudness of the sound. Conversely if the rate of action potentials decreases, the sound becomes louder. A calibrated microphone (Western-Electric 640 AA) placed adjacent to the leg measures the sound pressure. The microphone output is amplified, filtered, and recorded on a General Radio Graphic-Level Recorder, which is mechanically coupled to the oscillator frequency control. By this technique, a graph of the sound pressure at the leg as a function of the frequency can be rapidly and accurately obtained. The graphs that result from this procedure do not represent exactly the threshold of the preparation. This is mainly due to a slight amount of adaptation that occurs as each frequency is scanned. This tends to reduce the apparent sensitivity of the preparation. But the graphs do represent contours of equal rates of action potentials. Thus the equipment can be adjusted to measure the 5 action potentials per second contour or the 200 action potentials contour or anything between. At a rate below 20 action potentials per second these graphs are almost identical in appearance to those obtained by a true threshold measurement. The thresholds reported in this paper represent 10 action potentials per second.

By slightly altering the arrangement of the equipment above it is possible to maintain a constant sound pressure at the leg and to record the rate of nerve action potentials as a function of frequency. This technique has the great advantage that small differences in receptor sensitivity are easily detected, whereas with the other technique differences are greatly compressed.

Sound levels reported in this paper are given in db.; o db. is equal to a sound pressure of 0·0002 dyne/cm².

Vibrations of insects in spider webs

Spiders were allowed to spin their webs in cardboard boxes in the laboratory. Various insects were captured in the field and released in the boxes. They soon became entangled in the webs and their vibrations were recorded with a vibration pick-up made from a crystal phonograph cartridge equipped with a glass probe. The output of the crystal was amplified and stored on magnetic tape. Air-borne sound was detected with a calibrated condenser microphone and similarly recorded. The tape was then cut into short loops and analysed with a General Radio Sound Analyser or with a Kay Sonograph. Because the vibration transducer was not calibrated, the

absolute form of the curves obtained from the frequency analyses of the insect vibrations is probably not significant. The differences found for the different insects are probably real.

Behaviour

The behavioural experiments were conducted on populations of wild spiders. The test insect was allowed to become ensnared in a web by being released nearby. The behaviour of the spider was noted. Many of these experiments were photographed on motion picture film with electronic flash. The analysis of the film as well as direct observations provided the data upon which the conclusions in this paper are based.
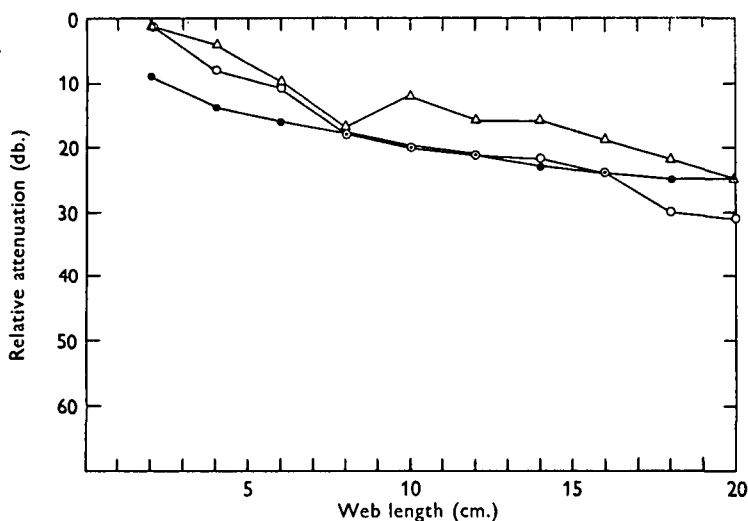

Fig. 2. The relationship between the attenuation of web-borne vibration and the length of the silk web strand. Each point represents a different web segment; each of the three lines represents silk from a different individual spider. The differences between the curves are probably due to variations in the tension of the silk.

RESULTS

Web transmission

The web of *Achaearanea* is a loose three-dimensional framework of silk strands. An average web may contain from 200 to 500 or more strands with an average length of 20 cm. each. The strands have a diameter of about 3μ.

An insect snared in a web sets up a considerable vibration. The question is how effective the web strands are in transmitting this vibration to the waiting spider. It appears that if the end of a strand of silk is vibrated, the vibration is transmitted along the length of the strand. But the amplitude of the vibration decreases as the length of the strand and thus the distance from the source increases (Fig. 2). The attenuation of the web strand is between 1·2 and 1·5 db./cm. This measurement was made with the web at 'normal' tension. Decreasing the tension to zero stops transmission while increasing the tension lowers the attenuation to 1 db./cm. just before the strand breaks.

These measurements were made at a frequency of 500 cyc./sec. Changing the frequency (Fig. 3) reveals that between 50 and 2000 cyc./sec. there is little variation

in attenuation with a change in frequency. On the basis of these measurements, it appears that spider silk is a relatively efficient transmission line for vibrations.

Vibration of the leg by the web

If vibrations are efficiently transmitted through the web, what is the response of the spider's vibration receptor to this source of stimulation?

One of the striking characteristics of this sense organ is its great variation in sensitivity to only slightly different frequencies of sound. But these variations disappear if the leg is cemented to a crystal and thus forced to vibrate. Since a spider in
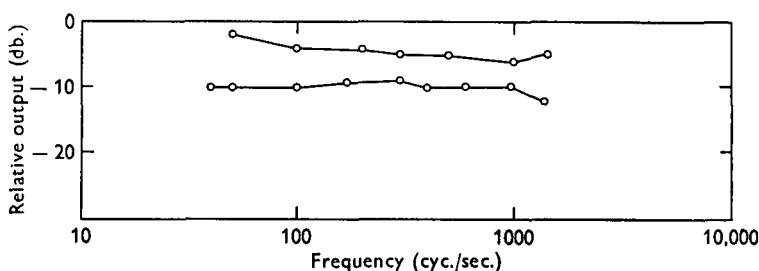

Fig. 3. The change in the attenuation of vibration transmitted by spider silk at different frequencies.
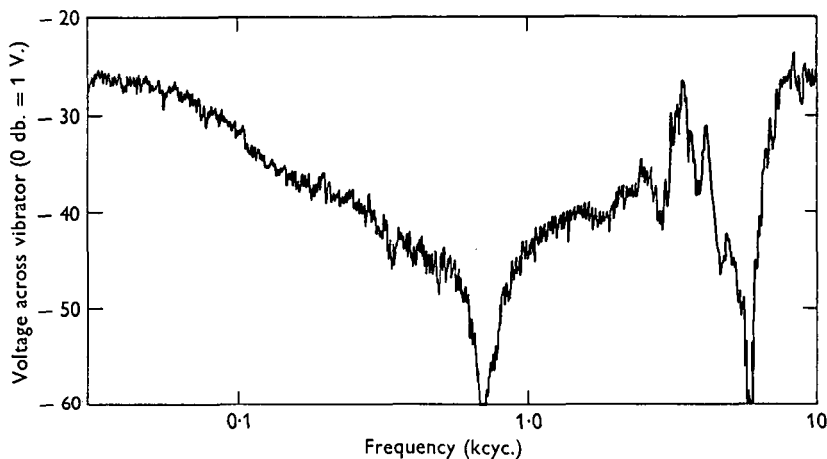

Fig. 4. The threshold of the response of the isolated spider leg to different frequencies of vibration transmitted directly to the leg tip via a single strand of spider silk. The peak at 7000 cyc./sec. is an artifact which probably represents a resonance peak in the crystal vibrator.

its web is in a situation that resembles the direct vibration experiments, it becomes a matter of great interest to see whether the peaks in the frequency response curve occur in response to web-borne vibrations.

To answer this question the tip of the leg was attached to the web strand and the electrical activity of the sense organ was followed.

First, the threshold of the preparation was determined for frequencies between 20 and 10,000 cyc./sec. The results of this measurement, shown in Fig. 4, reveal a relatively uniform threshold, with a gradually increasing sensitivity as the frequency

is increased. The threshold appears to reach a minimum at about 700 cyc./sec. and then to increase sharply once again. None of the dramatic changes in sensitivity to slightly different frequencies appears; the response is untuned.

If the threshold response seems to be uniform, is there any evidence of frequency discrimination by the receptor units?

Using the same preparation as before, the nerve impulses were sorted into five arbitrary groups on the basis of their height. In this way the activities of the different fibres could be followed. There is no reason to think that each channel represents the
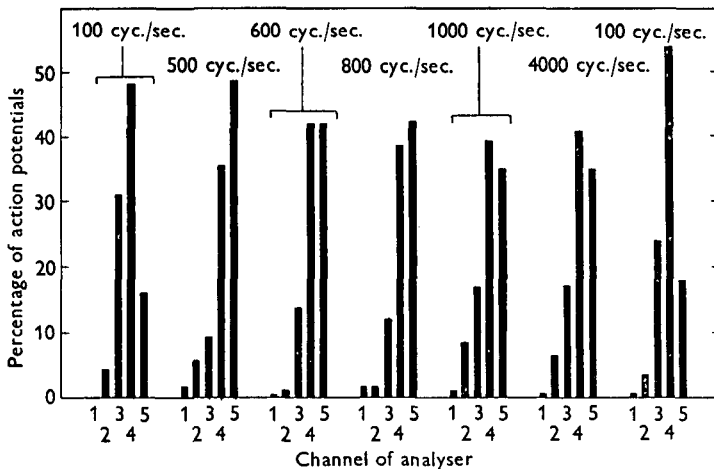

Fig. 5. The distribution of action potential heights in response to various frequencies of direct vibration. The response seems to be similar at all frequencies tested.

activity of a single receptor unit, but clearly a receptor counted in the lowest channel is not the same as one counted in the top channel (see Walcott & Van der Kloot, 1959). The relative activities of the five channels were determined for several frequencies of web-borne vibration and the results are shown in Fig. 5. These results indicate that there is little or no variation in the activity of the different receptors with different frequencies of web-transmitted vibration.

By adjusting the analyser it is possible to follow the activity of a very narrow range of pulse heights. The activity of a single channel with this arrangement probably does represent the activity of a single receptor unit or at most two receptor units. Measuring the rate of impulses appearing in a single channel as the frequency of vibration is changed shows that the threshold of any one channel duplicates almost precisely that of the preparation as a whole (Fig. 6).

Both of these results indicate that for vibrations transmitted via the strands of the web, the sense organ provides no information about the frequency of the vibration. This failure to discriminate frequencies might be due either to the attachment of the leg tip to the spider web or to the fact that the vibrations are transmitted directly by a web strand.

Response of the leg and the web to sound

To decide between these alternatives the leg was arranged as before with its tip on the strand of silk. Now, however, the preparation was stimulated with air-borne sound. The threshold of the preparation to various frequencies of sound is shown in
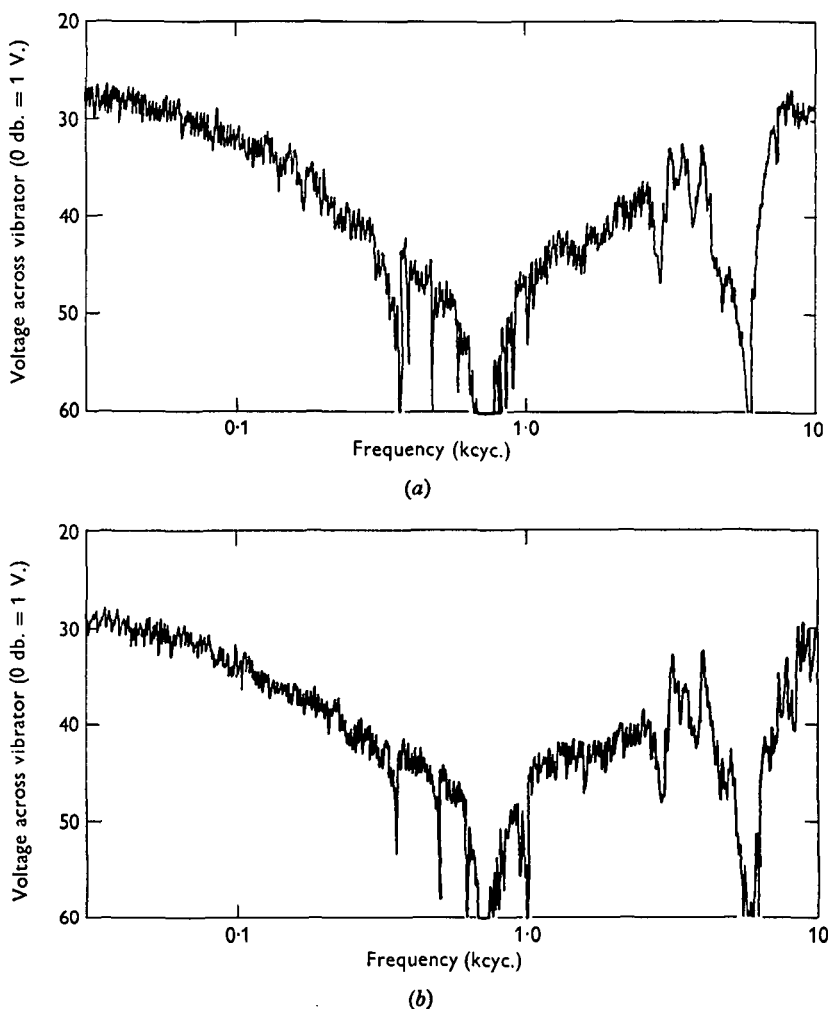

Fig. 6*a*, *b*. The threshold response of the leg to vibration transmitted directly to the leg by a strand of the web. Only those action potentials that were counted in channel 2 of the analyser are shown. This probably represents one receptor unit or at most a few receptor units. Fig. 6*b* shows the threshold of channel 4. The response of both of these single channels is essentially the same and very similar to that of the entire preparation as shown in Fig. 4. Compare these results with the response to air-borne sound shown in Fig. 9.

Fig. 7. Clearly the variation in sensitivity to closely adjacent frequencies is now present. In fact, the slope of the sensitivity peak at 155 cyc./sec. is about 3 db./cycle of frequency change which is as great as that found when the leg tip is free.

An examination of the activity of the five groups of action potential heights (Fig. 8) shows that the activity varies from one frequency to another. This implies that

frequency discrimination is occurring in response to air-borne sound even with the leg tip attached to the web. Following the activity of each of these five groups of action potentials, as the frequency is changed (Fig. 9), reveals that each channel is 'tuned' to more than a single frequency. But the threshold of the receptors to these frequencies varies from one channel to another. That these channel-to-channel differences are
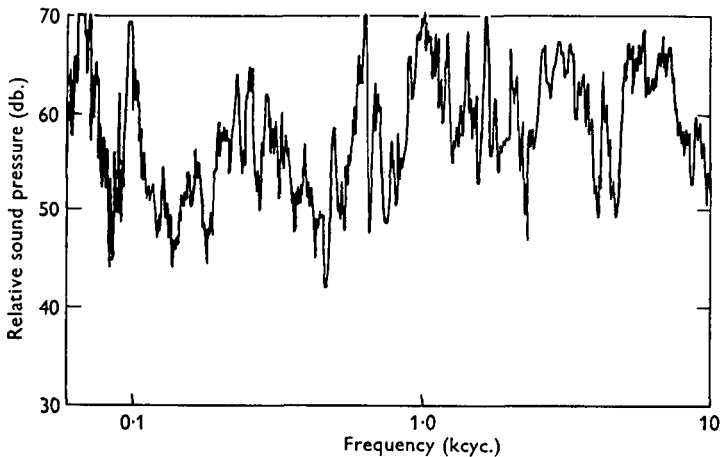

Fig. 7. The threshold response of the leg with its tip attached to a web strand. The stimulus was air-borne sound. This graph, taken from the automatic scanner, diminishes the sharpness of the peaks and reduces somewhat the contrast in the response of the sense organ to the most and the least stimulating frequencies.
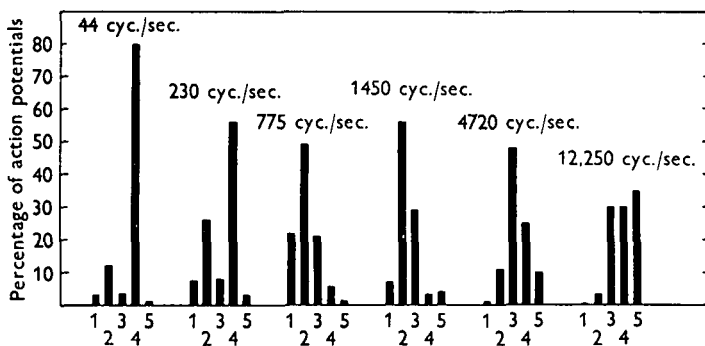

Fig. 8. The distribution of action potential heights for various frequencies of air-borne sound with the leg tip attached to the web.

not due to a change in the sense organ's properties as the preparation ages is shown by the reproducibility of these curves. The response of channel 1 is essentially similar no matter where in the sequence of measurements it occurs.

Previous work (Walcott & Van der Kloot, 1959) had suggested that the position of the leg and the tightness of its coupling to the source of vibration had an effect upon its tuning. To measure the effect of altering the tension between the leg tip and the web strand the response of a single fibre was monitored by a single channel of the analyser. The threshold of this preparation to the frequencies around 470 cyc./sec. was measured (Fig. 10). The result of this measurement was to disclose a peak of
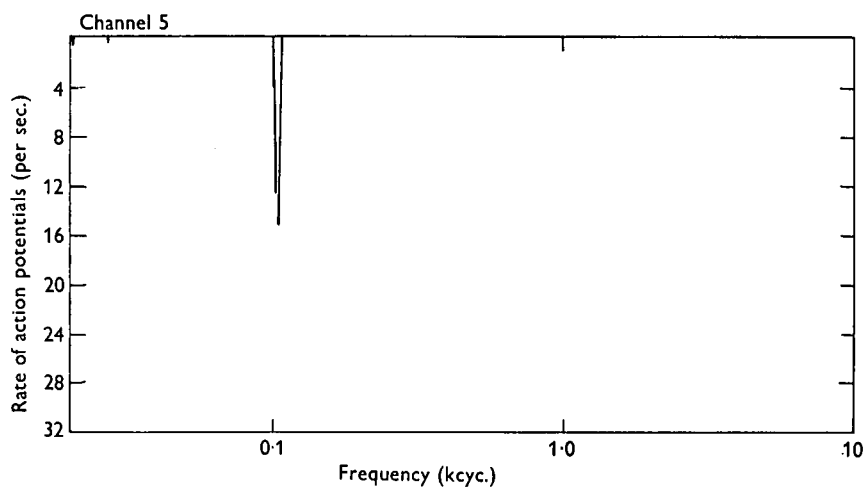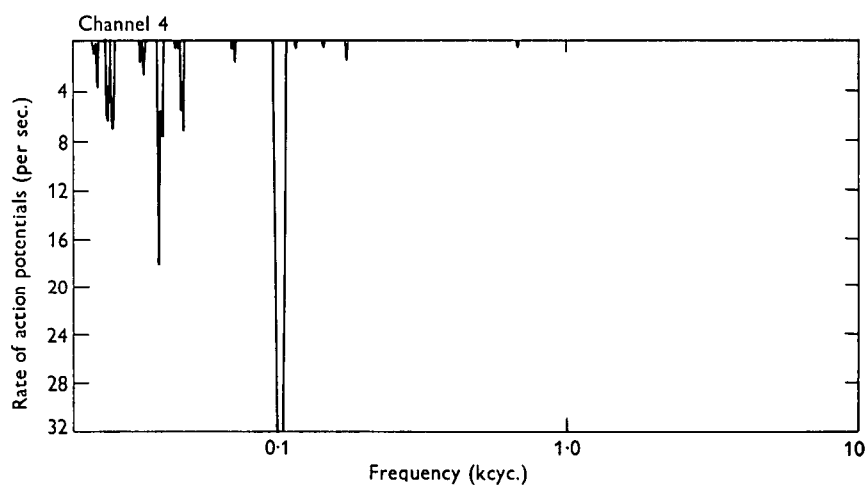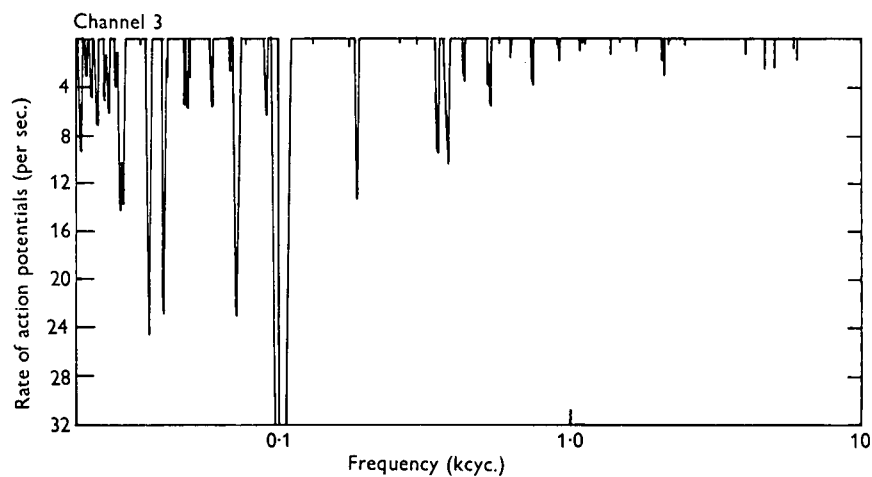
Fig. 9. For legend see opposite page

maximum sensitivity at 470 cyc./sec. The slope of this peak was 1·2 db./cycle of frequency change and the minimum sound pressure necessary to elicit a rate of 10 action potentials per second was + 52 db. at 470 cyc./sec. The tension between the leg tip and the web strand was now increased to just below the breaking point of the
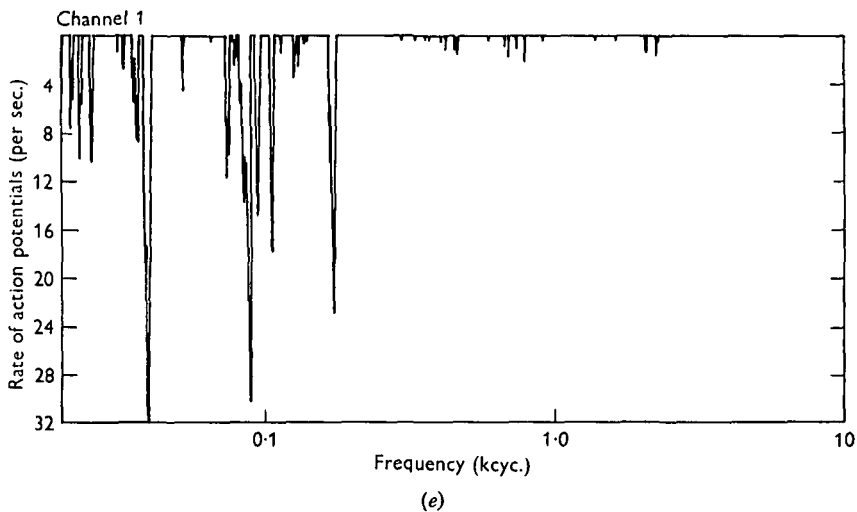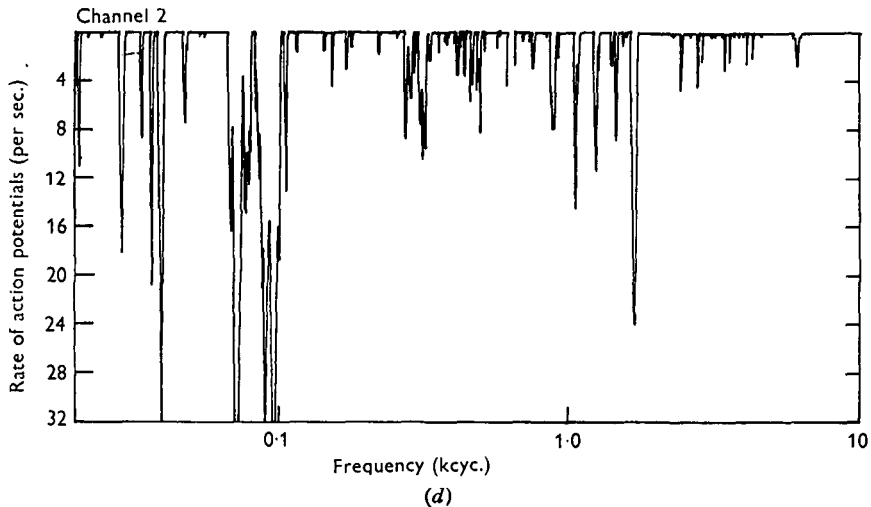

Fig. 9*a, b, c, d, e*. The responses of the five channels of the pulse-height analyser to various frequencies of air-borne sound. The sound level was maintained constant at + 50 db. The action potentials with the highest voltage were counted in channel 5, the lowest in channel 1. In this experiment it is probable that more than one receptor unit was recorded in each channel.

web strand. Again the threshold was measured. With greater tension, the threshold had decreased from + 52 db. to a low of + 36 db.; a decrease of 16 db. At the same time the slope of the peak had decreased slightly to 1·0 db./cycle of frequency change. This result shows that the tension between the leg and the web strand has a large effect upon the sensitivity of the preparation to air-borne sound, but relatively little effect upon the sharpness of the tuning of the receptor unit.

39

But there is additional variation in sensitivity found when recording from the leg of a live spider. Even if the leg is carefully fixed in position, so that the tension between leg and web cannot vary as the spider struggles to free itself, the sensitivity changes markedly. These changes appear to be correlated with the movements of the other
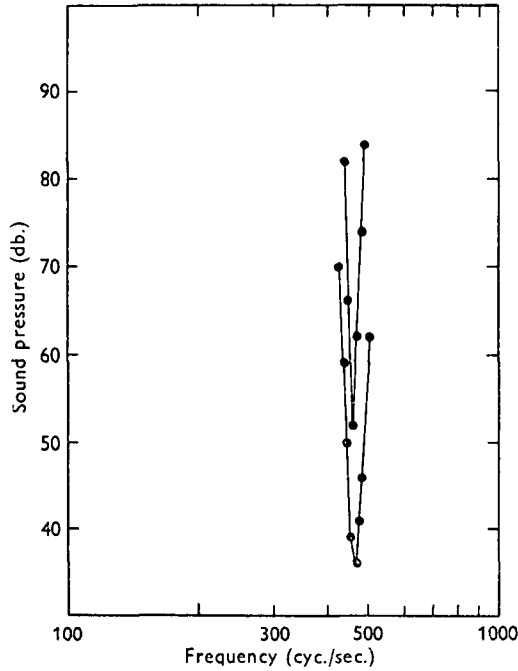

Fig. 10. The change in the threshold response to air-borne sound that occurred in a single receptor unit as the tension between the leg tip and the web strand was increased. The upper curve was 'normal' tension; for the lower curve the tension was increased.
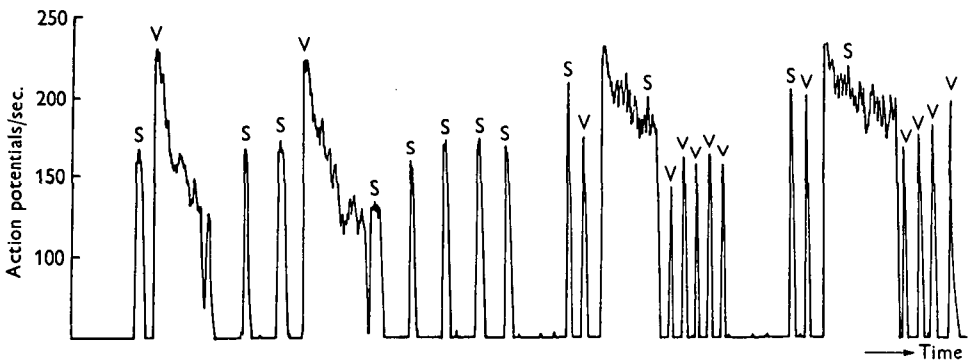
Fig. 11. The effect of adaptation of the sense organ by vibration on its response to air-borne sound and the effect of air-borne sound on its response to vibration. The sound was +70 db. at 700 cyc./sec. and the voltage across the vibrator was 40 db. below 1 V. at 700 cyc./sec. S, Air-borne sound; V, web-borne vibration.

legs. They were never found in the isolated leg. Neither the variation in sensitivity due to the leg-web coupling nor that described above were found in preparations responding to direct web-borne vibrations.

The results reported so far suggest that two separate receptor systems might exist in the leg; one receptor might respond to air-borne sound with sharp tuning and frequency discrimination, the other might respond only to direct vibration. To test this suggestion we arranged an intact spider so that the leg from which the electrical recordings were made was attached to the web strand as usual. It was possible to stimulate the leg with either air-borne sound or direct vibration and to switch rapidly from one to the other. The receptor was now exposed to a sound that elicited a rate of several hundred action potentials per second. A short burst of this sound was followed by a period of vibration transmitted via the web. After about 30 sec. of vibration the response to sound was reduced, and it could be concluded that the vibration had adapted the receptor to air-borne sound. That this is indeed the case is shown in Fig. 11.

Furthermore, as shown in Fig. 11, the response to direct vibration can be reduced by a previous exposure to air-borne sound. These results suggest that the same receptor is responsible for sensitivity to both web-vibration and air-borne sound.

Frequency of insect vibrations in spider webs

The experiments so far described have shown that the spider's vibration receptor provides some information about events occurring in the web. Since it seems highly likely that the spider uses this information to locate insects snared in its web, it now becomes of interest to see what sort of vibrations are actually caused by a struggling insect. Even to the casual listener the sound of a honey bee (*Apis mellifica*) tangled in a spider web is noticeably different from that made by a house fly (*Musca domestica*). But it might well be that, in spite of this apparent distinction, the distribution of energy among the various frequencies of sound and vibration is not greatly different, or that the vibration transmitted directly via the strands of the web differs significantly from the air-borne sound.

The vibrations and sound produced by both honey bees and house flies snared in webs were recorded and analysed. The frequency distribution of the air-borne sound was essentially identical with that recorded directly from the web and therefore only the latter is presented here (Figs. 12, 13). As an inspection of the data shows, there is a clear cut difference between the vibrations of a bee and those of a fly. The honey bee, for example, produces a significant amount of energy at frequencies near 1 kcyc. The house fly produces greater energy at lower frequencies.

Behaviour of spiders

From these experiments it appears that, at least for the honey bee and the house fly, there are distinct differences in both the sounds and the vibrations which insects produce when tangled in a web. On the basis of the electrophysiological data one would expect the spider to be able to detect this difference if it were responding to the air-borne sound but not to be able to do so to the web-borne vibration. It seemed possible that observing the behaviour of spiders in their webs towards these insects might furnish a clue as to which of these modes was the more important to the spider.

To examine this question both honey bees and house flies were released near webs, and when they became ensnared the spider's response was recorded. Our experiments reveal no consistent differences in the spider's treatment of the different insects in

its web. Such measures as the time required to initiate an attack, the direction of the attack, and the time required to reach the prey were no different for a honey bee than for a fly. When the spider reached its captive, by contrast, its behaviour did change, but by that time it was impossible to rule out the effect of chemical and tactile stimuli.

These behavioural experiments suggest that either the spider is unable to detect the differences in the vibrations produced by bees or flies, or that, if it can do so, it makes no obvious use of the information.
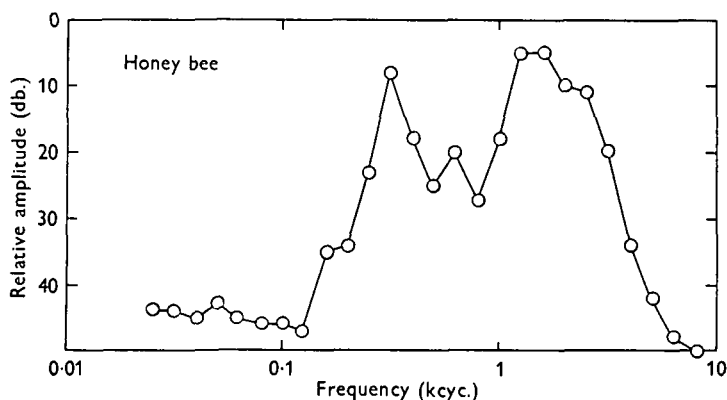

Fig. 12. The relative amplitude at various frequencies of the vibrations caused by a honey bee snared in a spider web.
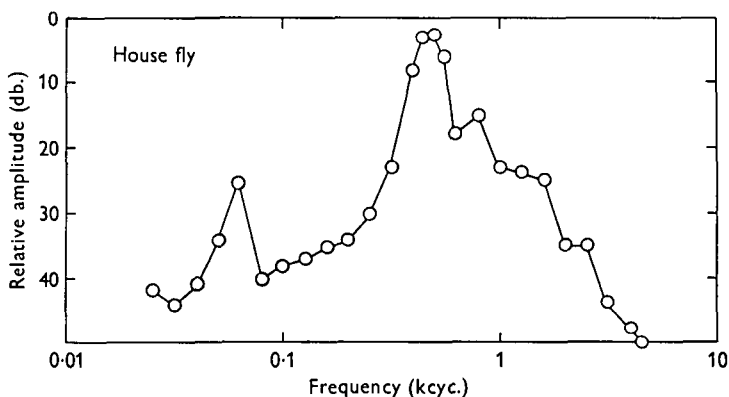

Fig. 13. The relative amplitude at various frequencies of the vibrations caused by a house fly snared in a spider web.

DISCUSSION

It has been shown that spider silk is an effective transmission line for vibrations. No analysis has been made of vibration transmission in the whole web of *Achaearanea*, but Liesenfeld (1956) has made a detailed analysis of the vibration pattern of the web of *Zygiella*. Since the web of *Achaearanea* is an irregular meshwork of threads, presumably vibration of the web as a whole rarely occurs. In an orb web of the sort spun by *Zygiella*, each web strand is attached to many others in a single plane. Vibrations of a single point of the web should spread in a systematic fashion over the entire web.

In the irregular mesh of *Achaearanea* no such spread will necessarily occur. Each strand meets only a few others and the spread of vibration from a struggling insect in the web is thus far more irregular and can only be guessed at from the studies on single web strands. The average *Achaearanea* web has strands of about 20–30 cm. long. Thus, if there is no added attenuation due to the attachment of other strands, vibrations might be attenuated by 45 db. in traversing the web. This figure is probably a minimum estimate, for there almost always are several other connected strands. Such an estimate shows clearly why the spider's vibration receptor is so sensitive.

Direct vibration of the leg by the web

The finding that the sense organ responds with almost uniform sensitivity to vibrations of a wide frequency range when they are transmitted directly through the web is not surprising. The previous experiments (Walcott & Van der Kloot, 1959) where the leg was forced to vibrate with a crystal also showed a failure of the 'tuning' found in the sense organ's response to air-borne sound. Furthermore, the work of Liesenfeld (1961) has shown that *Zygiella* also has a relatively uniform frequency response curve for direct vibration. He finds none of the peaks that characterize *Achaearanea*'s response to air-borne sound.

The lack of apparent frequency discrimination in the receptor units could also be predicted from the work with the crystal vibrator. Whenever the peaks in the threshold response curve disappear, it seems that the discrimination of the individual receptors does also. The failure of the receptors to discriminate the web vibration frequencies is surprising, for it would appear that this information might be important to the spider. On the other hand, one can argue that a relatively uniform frequency response of the receptor system as a whole is of even greater value.

When the leg, with its tip attached to a web strand, is exposed to air-borne sound, both the peaks in the response curve and the frequency discrimination of the receptor units reappear. That these peaks are a consequence of standing waves or of other characteristics of the room in which the experiments were conducted seems unlikely; they were found even in the anechoic chamber of the Harvard Cruft Laboratory. That they are caused by a vibration of the electrodes, as suggested by Liesenfeld (1961), also seems improbable, for the electrodes were solidly embedded in plastic and the leg, except for the tarsus, was carefully immobilized. The only conclusion that seems tenable is that both the peaks in the threshold curve and the discrimination of the receptor units are a characteristic feature of the sense organ's response to air-borne sound.

Single receptor units appear to respond to air-borne sound of more than a single frequency. This result may well be an artifact caused by using the pulse-height technique to separate the activities of single units. But it seems more probable that this is a true feature of their response. How this tuning arises is very hard to understand, and the current investigation has thrown very little light upon this problem.

Tension

Increasing the tension between the leg and the web alters the preparation's sensitivity and to a lesser extent decreases the sharpness of the tuning. The 16 db. decrease in the threshold is probably due in part to increased transmission through

the web strand. For a 15 cm. segment of silk the attenuation under normal tension would be about 22 db.; increasing the tension to maximum would decrease the attenuation to about 15 db.: a change of +7 db. Clearly, then, the increased sensitivity cannot be solely attributed to the decrease in attenuation, but must also be a consequence of the change in coupling between the leg tip and the web strand. Quite possibly also the change in tension on the slits of the lyriform organ has had an effect.

The variation in sensitivity found in the live spider seems to be due to changes in the internal hydraulic pressure of the leg. Parry & Brown (1959) have shown that the extension of the spider's leg is accomplished by an increase in fluid pressure within the leg. Since in our experiments the leg was immobilized and the changes in sensitivity were correlated with the movements of the other legs it seems quite probable that changes in internal pressure were responsible for the alterations in sensitivity.

The behaviour of spiders towards insects

There is no question that different insects produce different frequencies of both air-borne sound and direct vibration when tangled in a spider's web. But it seems equally clear that either *Achaearanea* cannot detect these differences, or, if it does, it makes no obvious use of the information.

It might be argued that the response to air-borne sound and the response to web-borne vibration are mediated by two separate receptors. But Liesenfeld (1961) has shown, at least for *Zygiella*, that the tarsal–metatarsal lyriform organ is responsible for the sensitivity to direct vibration. Furthermore, Walcott & Van der Kloot (1959) have shown that it is this same sense organ which responds to air-borne sound. This conclusion is supported by the finding that air-borne sound and direct vibration both adapt the receptor. This is not surprising for surely a receptor system sensitive enough to respond to air-borne sound will also respond to direct vibration. The evidence thus suggests that the receptor is the same for both modes of transmission.

Bays (1962) reports that he has been able to condition *Araneus diadematus* to discriminate the frequencies of two tuning forks. The frequencies he used are described as C and C[1], which probably represent about 128 and 256 cyc./sec. respectively. This finding shows at least that *Araneus* can discriminate frequencies in this range, but unfortunately it does not make clear whether this is accomplished by using the information provided by direct vibration or by air-borne sound. A tuning fork produces both sorts of vibration and it must now be asked which of these modes of transmission was used by the spider to tell one fork from the other.

The failure of the spider to alter its behaviour to different species of insects snared in its web, and the absence of any differential response of the receptor units to web-borne vibration, raise a serious question. One can argue that the frequency discrimination of the receptor and the pronounced peaks in the frequency response curve which are found when using air-borne sound as a stimulus are just an accidental feature of a sense organ that is optimally sensitive to direct vibration. Perhaps sensitivity to air-borne sound has no meaning in the life of the spider. For it is surely true that spiders are primarily concerned with vibrations occurring within their webs, using them to locate prey or find their mates. Perhaps the response to air-borne sound represents the price the spider has to pay for optimum sensitivity to vibrations of its web.

This conclusion seems unlikely for two reasons. First, the sensitivity to air-borne sound is very great; a high background noise level should seriously interfere with the response to direct vibration of the web. Secondly, a preliminary study (Walcott, unpublished data) of other species of spiders reveals that most of the web spinners are very sensitive to web-borne vibrations, but only the species that spin the irregular webs characteristic of *Achaearanea* are sensitive to air-borne sound. This finding argues that high sensitivity to web-borne vibrations is not necessarily coupled with high sensitivity to air-borne sound.

Finally, Bays's report that *Araneus* could be conditioned to discriminate frequencies shows that at least one species of spider can so discriminate. Whether *Achaearanea* can be similarly conditioned and whether the response is to air-borne sound or to direct vibration will be interesting to see. Only a further examination of the spider's behaviour will tell us about the role of air-borne sound in the life of this species of spider.

SUMMARY

1. The contribution of the web to vibration sensitivity in the spider *Achaearanea tepidariorum* (Koch) has been examined. A single strand of web transmits vibration with an attenuation of about 1·2 db./cm. of silk.

2. The electrical activity of a spider leg, the tip of which was attached to a web strand, revealed no tuning in response to vibration transmitted via the web, whereas the response to air-borne sound was still tuned.

3. The behaviour of spiders toward different insects snared in their webs revealed no differences in the spider's initial response to the different insects, although the sound and vibration caused by the insects were clearly different.

4. These results suggest that the spider can derive more information from the air-borne sound than it can from vibration through its web, but what use the spider makes of its sensitivity to air-borne sound is still unclear.

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