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THE SIGNAL GENERATED BY AN INSECT IN A SPIDER'S WEB

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INTRODUCTION

It is generally accepted that web-spinning spiders detect and find prey in their webs through the mechanical signal generated by the prey. There is also a good deal of evidence that spiders discriminate between different types of signal. Barrows (1915) caused *Epeira sclopetaria* to orientate, or move, towards a tuning fork; and found the frequency-band of 24–300 cyc./sec. most effective. Meyer (1928) obtained responses from several species of Agriopidae (orb-web spinners) to a tuning-fork (435 cyc./sec.). Peters (1931), with *Epeira diademata*, found that the spiders did not respond to a dead fly placed gently in its web; if, however, the fly arrived in the web with a jerk or if, once in the web, it was suddenly tapped with a needle or stimulated with vibrating forceps, then the spider responded. Liesenfeld (1956) also found, with *Zygiella x-notata*, that a vibrator suddenly switched on would produce a response, while, if the amplitude of vibration was slowly raised, no response occurred. Walcott & Van der Kloot (1959) obtained responses in *Achaearanea* (= *Theridion*?) *tepidariorum* to a vibrating phonograph needle over the range 400–700 cyc./sec., while between 700 and 3000 cyc./sec. the spider retreated or dropped from the web. Tretzel (1961) similarly obtained responses from *Coelotes terrestris* to sinusoidal vibrations generated by a loudspeaker movement and drew attention to the ability of females to distinguish between prey and their own young. Most recently Bays (1962) has conditioned *Araneus diadematus* to discriminate between tuning forks vibrating at 262 cyc./sec. (= *c*) and 523 cyc./sec. (= *c*′).

In contrast to the amount of work on the response of spiders to sinusoidal and other artificial signals, there is little information about the natural signal generated by living prey. Liesenfeld (1956) analysed cinematograph records of flies moving in the web of *Zygiella* and recognized wing vibration, body movement and the resonance of the insect in the web as components of the movement pattern. Tretzel (1961, see above) tape-recorded signals from the web of *Coelotes* produced by prey and by young spiders, and compared their frequency content. He found that the signals produced by prey contained higher frequencies, and showed a greater range of intensities, than those produced by young spiders. But he doubted whether the spider's evident ability to discriminate between prey and young did in fact depend on frequency. Walcott (1963) published spectral analyses of recorded signals produced by bees and flies in the web of *Achaearanea* but found the energy distributed over a wide frequency range (mostly within 100–5000 cyc./sec.)

Thus we have evidence that various spiders discriminate between sinusoidal signals

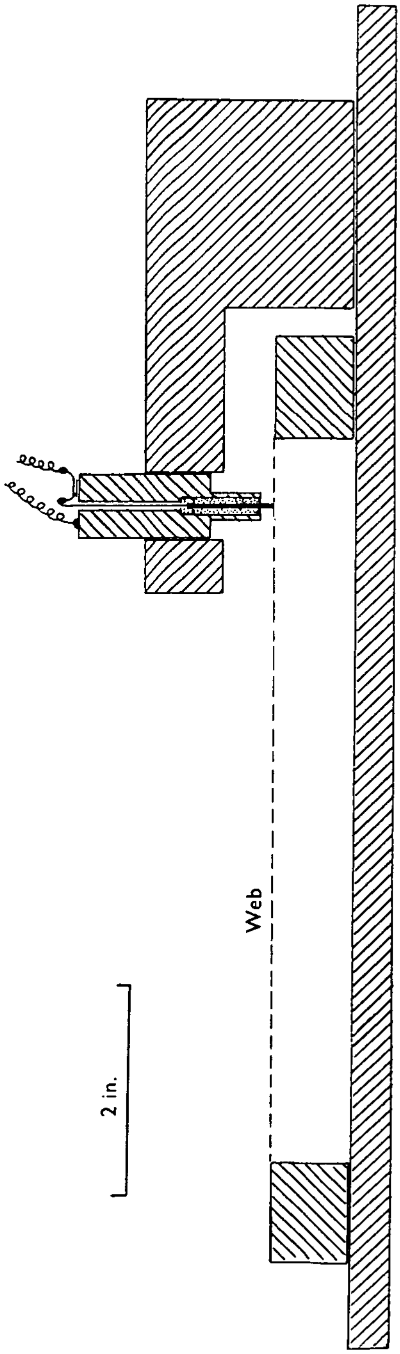

Fig. 1. For explanation, see text.

of different frequencies, and also evidence that they discriminate between living prey and artifacts. But there is little evidence that the latter discrimination (which has obvious selective advantage) is frequency dependent, neither is there any particular reason to suppose that the slight movement of insects in a web would produce a signal with some characteristic frequency spectrum. Clearly more information is needed about natural signals, and this paper contains a study of the vibration produced in the 'cobweb' of the British house-spider *Tegenaria atrica* by small cockroaches, which it readily detects and attacks.

METHODS

Spiders and webs. This work has been done on the British house-spider *Tegenaria atrica* (Koch) which readily spins its horizontal 'cobweb' in confinement. For experimental purposes the animals are given rings of wood (7½ in. inside diameter) and they build their webs across the ring. These can be bolted to a steel plate to which the transducer is also secured. Fig. 1 shows the layout.

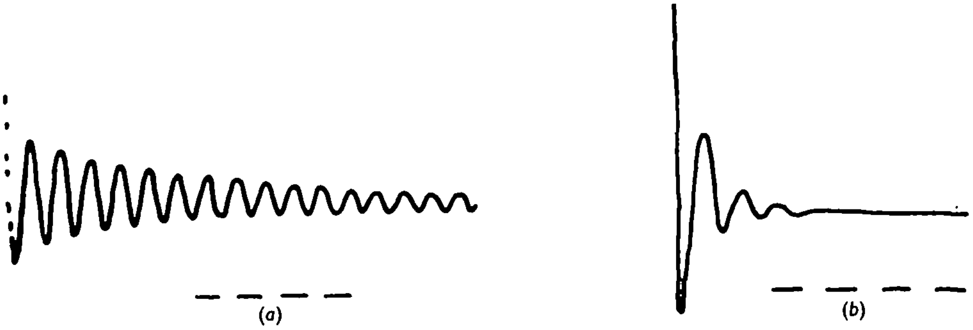

Fig. 2. Transducer response (*a*) undamped; (*b*) damped with silicone fluid, 1250 centistokes. Calibration: 1000 cyc./sec.

Signal source. When a small cockroach is dropped on the web it usually lies still for a time and then begins to make slight movements with legs and antennae. These movements are enough to provoke an attack if a spider is present; the spider runs across the web, in the direction of the insect.

A cockroach will make slight movements of this sort while recovering from CO_2 anaesthesia and it is the signal produced under these conditions that has been examined. Cockroaches approximately 10 mm. long (50 mg.) are anaesthetized and placed in the centre of the web. Recordings are made when movements begin, and are discontinued when the insect eventually starts walking across the web as the signal amplitude then exceeds the linear range of the pre-amplifier.

Transducer. This consists of a ½ in. length of PZT multimorph (Brush-Clevite Co.) used as a cantilever, and damped with silicone fluid (see Fig. 1). It has a resonant frequency of just under 2 kc./sec., and progressive damping was obtained with fluids of up to 12500 centistokes, but not beyond this viscosity.

The response was studied by dropping a ball-bearing on the end of the transducer; the ball triggering an oscilloscope trace, just before impact, through interruption of a light beam. Fig. 2*a* shows the response of the undamped transducer; Fig. 2*b* shows the damped transducer as used in these experiments. The damping factor is very approximately 0·45 ($Q = 1$) and the sensitivity 1·75 mV/dyne.

Electronics (see Fig. 3). The transducer is RC-coupled to a Tectronix pre-amplifier (× 1000, maximum unbalanced input ± 5 mV). The output is fed to a Telequipment oscilloscope and can also be monitored aurally through headphones.

The gain is flat (± 3 db.) from 2 cyc./sec. to 30 kc./sec., calibration being carried out with a sinusoidal signal fed into the cathode follower through a capacitance of 840 μF. which is equal to the capacitance of the transducer.

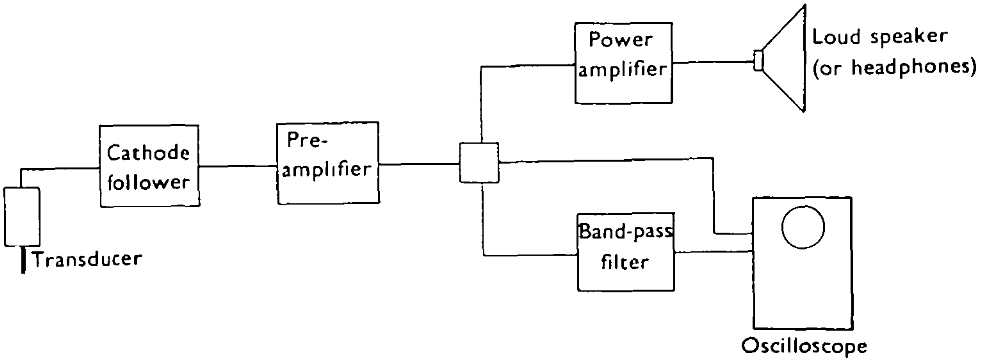

Fig. 3. Diagrammatic lay-out.

To avoid distortion due to the mechanical resonance of the transducer the signal was frequency-limited to 1 kc./sec., using the simple RC filter in the pre-amplifier. This signal is referred to as the 'broad-band' signal. For further frequency-limiting, a Krohn–Hite model 315 A variable band-pass/high-pass filter was used; and its output could be displayed on one trace of the oscilloscope while the broad-band signal was displayed on the other trace.

RESULTS

1. A typical broad-band signal is shown in Fig. 4, and further examples are given in Figs. 6 and 7 (upper traces). It is a very irregular wave-form but there are, nevertheless indications of a 60 msec. periodicity (equivalent to a frequency of 15 cyc./sec).

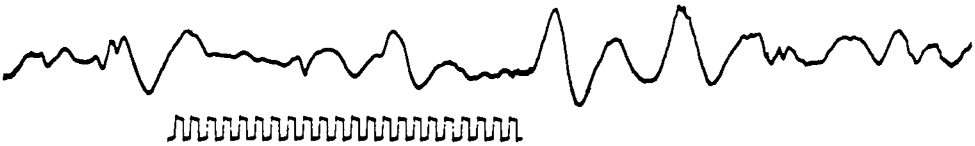

Fig. 4. Typical broad-band wave-form produced by an insect making slight movements in the web. Calibration: 50 cyc./sec.

This can be shown in the following way to be the period of the transverse oscillation of the insect in the web. The cockroach, from which the records of Figs. 4 and 6 were made, was killed and placed in the centre of the web. A small glass bead was dropped on to it and the resultant signal recorded—Fig. 5 (*a*). It is a heavily damaged oscillation with a period of 60 msec.

2. Fig. 6 shows (upper trace) a broad-band signal and (lower trace) the same signal band-limited to 50–500 cyc./sec. and with a relative gain of × 5. An occasional periodicity of very approximately 10 msec. is evident on the lower trace; and this is the order of magnitude of the *rotational* oscillation of the insect in the web. The

evidence for this is shown in Fig. 5(*b*), which is the signal recorded whan a glass bead is dropped ***excentrically*** on a dead cockroach to emphasize the rotational oscillation. The upper, broad-band, trace shows the transverse oscillation as in Fig. 5(*a*). The lower trace (band-limited to 50–500 cyc./sec.) shows a damped oscillation with a period of about 10 msec. (equivalent to 100 cyc./sec.).

3. Fig. 7 shows (upper trace) a broad-band signal and (lower trace) the same signal band-limited to 200–500 cyc./sec. and with a relative gain of × 5. The band-limited

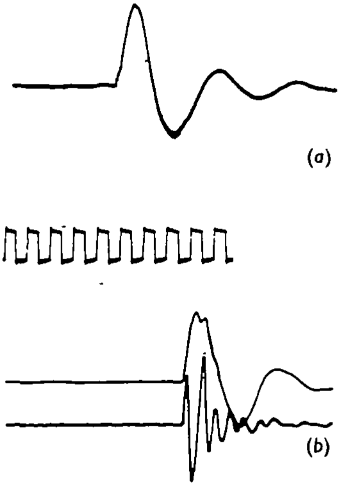

Fig. 5. Response of a dead insect to an impulse (glass bead). (*a*) broad band. (*b*) upper trace: broad band; lower trace: band limited to 50–500 cyc./sec. Calibration: 50 cyc./sec.

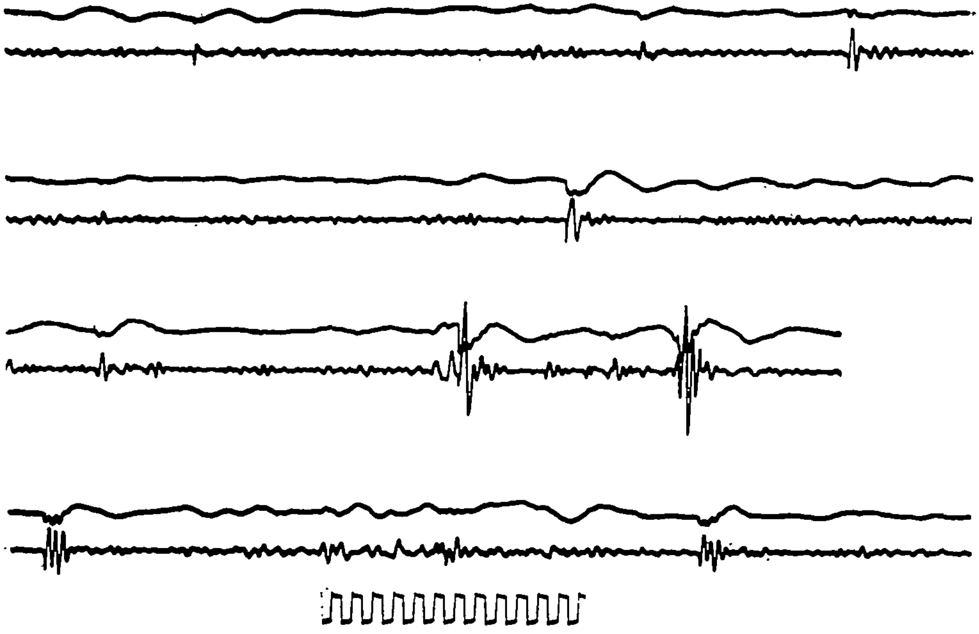

Fig. 6. Typical wave-forms produced by an insect making slight movements in the web. Upper trace: broad-band; lower trace: band-limited to 50–500 cyc./sec. Calibration: 50 cyc./sec.

signal is characterized by sporadic pulses which can be seen to correspond to sudden discontinuities in the broad-band signal. Similar discontinuities can be seen in Fig. 6, and one such discontinuity is particularly well shown in Fig. 8. Fig. 7 (4th row) shows a burst of 'activity' in the narrow-band channel; but note that the occurrence of discontinuities is not obviously related to the intensity of the broad-band signal. This is well shown in Fig. 7 (5th row) where the broad-band signal amplitude becomes very large but is only accompanied by a few pulses.

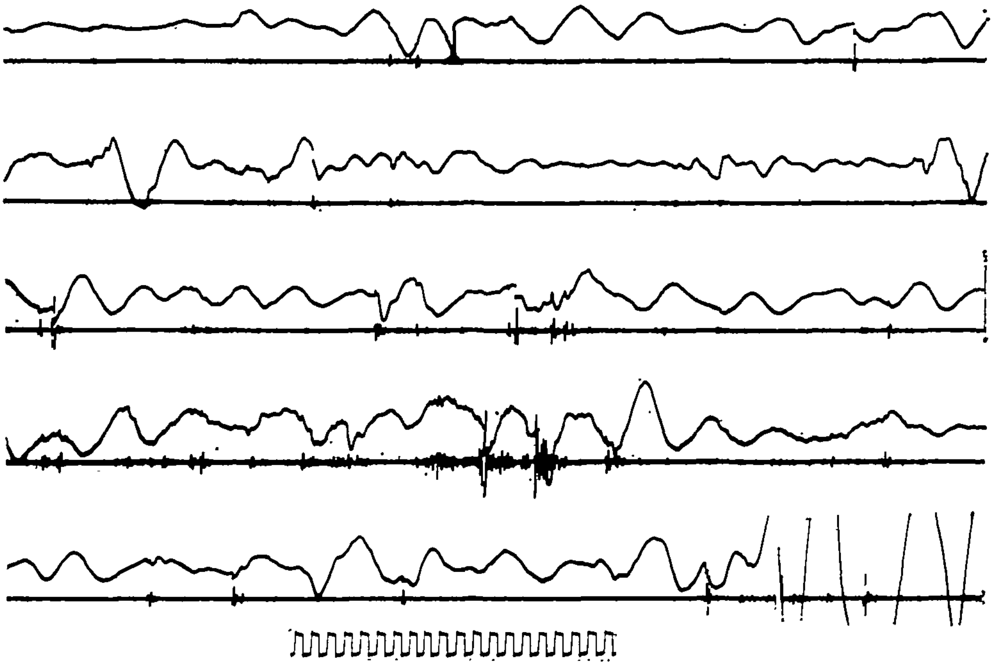

Fig. 7. Typical wave-forms produced by an insect making slight movements in the web. Upper trace: broad band; lower trace: band-limited to 200–500 cyc./sec. Calibration: 50 cyc./sec.

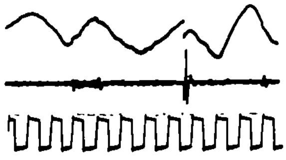

Fig. 8. Example of a 'fast transient'. Upper trace: broad band; lower trace: band-limited to 200–500 cyc./sec. Calibration: 50 cyc./sec.

DISCUSSION

The object of this investigation was to get information about the mechanical disturbance set up in the web of *Tegenaria* by an insect making the sort of movements which normally evoke the spider's attack response. These movements will bring the insect's limbs into impulsive contact with threads of the web, and it is not surprising, therefore, that the resultant wave-form is very irregular. It is dominated by low-frequency components (in the order of 10 cyc./sec.) which are due to the transverse oscillation of the insect in the web. There is also evidence of a higher-frequency component (in the order of 100 cyc./sec.) due to rotational oscillation. But possibly the most significant—and certainly the most unexpected—feature of the signal is the sporadic occurrence of discontinuities which will be referred to as 'fast transients'. The same effect can be obtained (Fig. 9) by moving an insect's leg or antenna, or a light string, very gently in the web with a micromanipulator. The precise cause of the fast transients is not known. They could be due to threads of the web being displaced by the insect and then suddenly snapping back into position. Alternatively, they might break or, more likely, suddenly become detached from the rest of the web which would then move into a new equilibrium position. Pl. 1 shows that the threads do not run in straight lines from one edge of the web to the other, but are attached to one another to form a complex network. This network is under tension, due to the way it is produced and also the to fact that it is weighed down by the insect. In normal use it may also be tensioned by the spider itself which has a characteristic way of standing on the dege of the web (often in a 'lair') and grasping a bundle of threads in the claws of its front pair of legs. If the insect's movements have the effect of releasing some of the tension, then the web is acting as an alarm system in which the energy is coming from the web itself and the insect is merely triggering its release. This could form the basis of a very sensitive detector.

Fig. 9. Insect antenna gently drawn across the web: band limited to 200–500 cyc./sec. Calibration: 50 cyc./sec.

The possibility that the fast transients form the basis of the spider's recognition of prey in its web is now being investigated.

SUMMARY

1. There is evidence that web-spinning spiders discriminate between prey and artifacts in their webs, and that the signal involved is a mechanical one. As a contribution to our understanding of the basis of this discrimination, an analysis has been made of the natural signal generated by an insect in the web of the British house spider *Tegenaria atrica.*

2. The signal investigated was frequency-limited to 1 kc./sec., this being the upper limit of the linear response of the specially designed transducer.

3. The signal has an irregular wave-form with most of the energy lying below 50 cyc./sec. Damped transverse and rotational oscillations of the mass of the spider in the compliance of the web have been recognized. In addition there are 'fast transients', most likely due to the sudden release of tension in the web by slight movements of the insect.

4. The possibility that the fast transients form the basis of prey-recognition is being investigated.

I am indebted to Dr K. E. Machin for a number of helpful discussions in the course of this work and for reading the manuscript. Some of the work was done while I was a visiting lecturer at Harvard University, Mass., U.S.A.; and I am particularly indebted to Prof. J. H. Walsh for the hospitality I enjoyed while working in the Harvard Biological Laboratories.

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EXPLANATION OF PLATE

Part of the web of *Tegenaria atrica*, illustrating the attachment of threads to one another, and their varying sizes.

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