VIBRATIONS AND SPIDER BEHAVIOUR

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Like all other animals spiders live in their own specific world. Their sense organs and central nervous system give them a strongly filtered view of their environment.If we want to understand spider behavior we have to find out what the world looks like to a spider.

Spiders have a sense of smell and taste,also a sense of touch. Most spiders have well developed eyes and some of them like the jumping spiders have superb vision. In addition to having all these sensory capacities they depend to a particularly large extent on signals and a sense which are of only limited significance in our own human experience. Spiders live in a world full of vibrations (Barth 1981,1986).

This is well known to every naturalist who has watched an orb weaver preying on a fly entangled in its web. Vibrations produced by prey are of the same importance in the wandering spiders. These do not receive vibrations through the threads of a web but instead through plants or even the water surface,reminding us of water striders (Bleckmann and Barth 1984). Spiders also emit their own vibrations and use them,for instance,in their highly developed courtship behavior. Many of them stridulate,not unlike crickets and grasshoppers. In addition,orb weavers are known to be able of a kind of echolocation:They pluck the individual radii of their web and thereby localize prey or other particles weighing as little as 0.05mg (Klärner and Barth 1982).

Evidently the evolution of spiders has led to efficient ways to detect,to localize, and to recognize vibratory signals. The question to be asked here is: How can the guidance of spider behavior by vibrations be explained in terms of the properties of sense organs and the central nervous system? This is a very ambitious question. We are far from having complete answers to

it. So let me introduce our experimental animal and its courtship behavior to show the practical relevance of the question and to illustrate a few aspects which can be examined experimentally.

Cupiennius salei Keys. is a large wandering spider (body length up to ca.4cm,leg span up to 12cm).The genus comprises 7 species (Lachmuth et al.1985) all of which live in Central America and are closely associated with monocotyledonous plants such as bromeliads and banana plants (Barth et al.1988a). *Cupiennius salei* is night active.It leaves its shelter after sunset to prey or to court on its dwelling plant (Barth and Seyfarth 1979,Seyfarth 1980).

The *courtship behavior* which ensures the finding and recognition of a mate in the darkness on the plant is characterized by the following main steps(Rovner and Barth 1981). (**i**) The female releases one or several pheromones attached to her dragline. (**ii**) Upon contact with the female thread the male starts to emit a specific vibratory signal. (**iii**) The male signal travels through the plant and reaches the female which responds with her own vibratory signal. (**iv**) The female signal travels through the plant back to the male which then starts searching for the stationary female.

Thus,the spiders communicate reciprocally with the male being the mobile partner. The female pheromone(s) arouses the male in a rather species inspecific way. Male *C.salei* readily start to vibrate when exposed to the draglines of *C.getazi* or *C.coccineus* (Barth et al. in prep.). On the other hand,the female only responds to conspecific male vibrations (Barth et al.in prep.).The species specificity of the male vibratory courtship signal obviously serves the female to recognize the proper species of the male. The female's own vibrations mainly inform the male of the presence of a female motivated for reproduction and guide it to the female.

Among the more specific questions now obvious are the following: (**1**) How are the vibratory signals transmitted from the sender to the receiver through the plant? (**2**) Which are the vibration receptors and how sensitive are they? (**3**) Which are the

characteristics of vibrations the spider is normally exposed to in its natural environment and how can it distinguish them?

1. TRANSMISSION OF VIBRATIONS THROUGH THE PLANT

According to field observations and laboratory experiments male and female communicate over distances of more than 1m using their vibratory signals (Rovner and Barth 1981).The transmission properties of the plant can be studied by vibrating it experimentally with an electrodynamic vibrator. Frequency bands containing all the frequencies of interest were introduced into the plant and their spectra compared at various distances from the site of the vibrator. Thereby attenuation values are determined for the various frequencies as they travel through the plant (Barth 1985,Barth et al.1988b). One important result of such experiments is that the average attenuation is ca.0.3dB/cm. In other words:the amplitude of the vibration will measure one half of its original value after having travelled for about 20cm through the plant.Among the several types of waves potentially relevant in a vibrating plant *bending waves* could be demonstrated to be of particular importance.These are identified by their main plane of movement (perpendicular to surface) and their low speed of propagation. The physics of plant vibrations is complicated by the dispersive nature of their propagation and by heterogeneities of the plant itself (Michelsen et al.1982,Barth 1985a,Barth et al.1988b).

2. VIBRATION RECEPTORS

There are several vibration sensitive sensilla in spiders (Speck-Hergenröder and Barth 1988).The most elaborate and sensitive vibration sensitive organ is the *metatarsal lyriform organ* (fig.1). Its cuticular slits are oriented at right angle to the long axis of the leg.The sensory cells attached to the slits are stimulated by slit compression which results from tarsal movements due to the vibration of the substrate. Electrophysiological

recordings from individual slits of the metatarsal organ of *C.salei* (Barth and Geethabali 1982) have shown us the following:
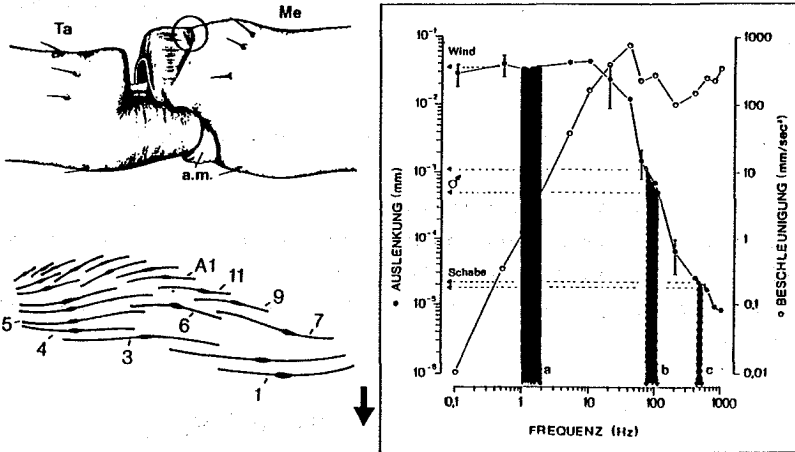

Fig.1 Metatarsal lyriform organ of C.salei. Left:position of organ (circle) distally on the metatarsus (Me) and dorsal view of organ to show the arrangement of slits. Arrow points toward the tarsus (Ta). a.m. articular membrane. Right: representative threshold curve of an individual slit.x-axis:frequency of tarsal displacement by vibrator; y-axis: displacement (left) and acceleration (right). Vertical bars indicate prominent peaks in the spectra of different types of natural vibrations (wind,male courtship,prey).(From Barth 1985,1986)

The threshold sensitivity of the organ is very high;at 1kHz it reaches values down to 10^{-6} - 10^{-7}cm (displacement of tarsus). The sensitivity of the metatarsal organ together with the attenuation values measured for the vibrations on their way from the sender to the receiver nicely account for the long distance of 1m or even 1.5m between the communicating partners. Another important finding relates to the shape of the threshold curve.The slits are not tuned to a particular frequency within the biologically relevant frequency range.Rather they behave like *high pass filters*. This implies low sensitivity at low frequencies between ca.10 to 40Hz (thresholds ca.10^{-3}-10^{-2}cm) and increasingly higher sensitivity at higher frequencies (above 40Hz threshold displacement values decrease by about 40dB/decade).

The same results were found when recording from the whole leg nerve of an unrestrained animal.Latest experiments have shown that some of the slits of the metatarsal organ are still considerably more sensitive than the ones so far examined (Baurecht, unpubl.).

3. NATURAL VIBRATIONS AND POSSIBLE MECHANISMS OF RECOGNITION

Who is it that vibrates? It is crucial for a spider to distinguish irrelevant background noise from prey signals. For a male courting on a plant it is life saving to be recognized as a conspecific male by the female and not to be confused by her with prey and eaten.
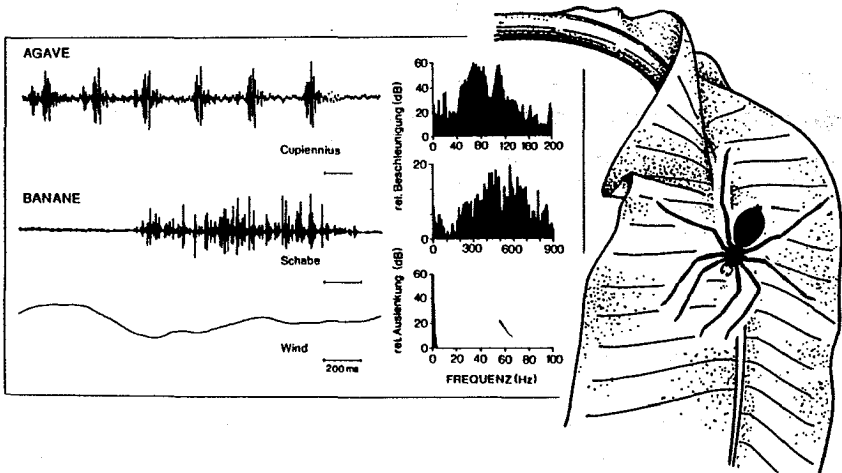

Fig.2 Representative examples of vibrations from the natural environment of C.salei. Left: oscillograms of male courtship signal,prey vibration (cock - roach),and plant vibration due to wind. Right: frequency spectra corresponding to the 3 types of vibrations. (From Barth 1986)

3.1 Differences between vibrations

We have measured various types of vibrations on the actual

dwelling plants of *Cupiennius salei* in Central America (Barth et al.1988b). Notwithstanding the variation in detail (varying plants,varying region on plant,varying distance and spatial relation between sender and receiver etc.) there are obvious differences among the main types of vibrations a spider is exposed to in its natural habitat (fig.2).

(i) *Background noise*: The most relevant source of background noise is wind. The vibrations it induces in a banana plant or a bromeliad have their main frequency component at very low values of about 1.4Hz.Frequencies higher than 10Hz show acceleration values 40 to 60db below the largest acceleration peak. Even with strong wind frequencies up to 40Hz have peaks at least 20dB below the maximum value. At -40dB frequencies up to 200Hz may be found.

(ii) *Prey vibrations*: Taking a cockroach running on a banana plant as an example we find that vibrations produced by prey animals are characterized by frequency spectra much broader than those of background noise and containing higher frequencies with peaks often between 400 and 700 Hz.

(iii) *Courtship vibrations*: The main frequency components contained in the male courtship vibration of *C.salei* are around 75Hz and 115Hz, those in the female vibration between about 20 and 50Hz. In addition, the male vibrations exhibit a prominent temporal patterning (Schüch and Barth 1985).

3.2 Recognition - prey,enemy or mate?

How do the spiders distinguish different types of vibrations? That they actually do make a difference can be easily observed. In essence,we ask for filter mechanisms which may be located both in the peripheral sensory system and in the central nervous system. Using ethological terminology we are asking for sign stimuli and releasing mechanisms.

(i) *Periphery*: As seen before the vibration receptors exhibit high pass characteristics,that is they are rather insensitive to low frequencies but increasingly sensitive to high frequencies. Marking the prominent frequency ranges of the various types of vibratory signals as shaded areas in figure 1 shows us that background vibrations fall within the range of low receptor sensiti-

vity.   It   is concluded that thereby the signal to noise ratio is
increased.In   other   words: biologically   irrelevant   background
vibrations   are   to a large extent kept out of   the   processing
system by the high pass characteristics of the sense organ.   The
sense organ forms the first stage of the filter we   are   looking
for.   Its   high   sensitivity at higher frequencies is taken   to
indicate the significance of these frequencies for courtship and
prey vibrations.

(ii) *Vibration sensitive interneurons*:   We are still far from a
complete understanding of what the central nervous system does
with the information it receives from the vibration   receptors.
Recordings from vibration sensitive interneurons in the suboeso-
phageal nervous mass of *C.salei*,which we assume to be at   least
close to the first stage of integration, led to some interesting
first answers,however (Speck-Hergenröder and Barth 1987). These
neurons all show band pass characteristics with a well pronounced
best   frequency   in   the   low   (80-100Hz,LF   neurons),middle
(ca.200Hz,MF neurons),or high (ca.900Hz,HF neurons) frequency
range. All these neurons were insensitive at low frequencies such
as those contained in background vibrations (fig.2). A remarkable
additional feature is the reduction of the threshold values by up
to   20dB when noisy stimuli (small frequency bands; width ca.1/3
of an octave) are used instead of sinusoidal ones. The main
conclusion from these findings is that the peripheral high pass
filter is   followed by a central nervous band pass filter which
selectively emphasizes frequency ranges of particular interest to
the animal.

(iii) *Behavior*:   The processes leading to a recognition of types
of vibrations cannot be uncovered by neurophysiological experi-
ments alone. To recognize in a way is to decide.If the spider
shows different behavior when exposed to different vibrations we
may assume a process of recognition to have been involved. Expe-
riments were carried out with the spider sitting on a platform
which consists of two halves: one immobilized,the other coupled
to a vibrator. With one or several (but not all) of its legs
resting on the vibrating half of the platform the spider shows
two types of behavior upon vibratory stimulation depending on the
properties of the vibratory stimulus. It either turns towards the

vibrating part of the platform as if it meant to catch prey or it turns away from it as if it would escape from it. The displacement thresholds for eliciting the "escape reaction" is higher than that for the "prey capture reaction" by about 20dB. Noisy stimuli (bandwidth ca.1/3 of an octave) reduce the threshold for "prey capture" by up to 10dB as compared to sinusoidal stimulation. The "escape response",however, is practically unaffected by this which is quite remarkable (Hergenröder and Barth 1983).

From these and similar findings we conclude that typical properties of effective prey signals are (a) a relatively low displacement amplitude, (b) non-sinusoidality,and (c) a composition by a broad spectrum of frequencies. As seen before prey vibrations differ just with regard to these properties from background vibrations. The importance of high frequency components in prey vibrations is underlined by the high-pass characteristics of the behavioral threshold curve.

These conclusions are nicely supported by observations of prey capture behavior in the field. Background vibrations due to wind (low frequencies,very narrow spectrum) never elicit prey capture even though the displacement amplitudes of such vibrations may be very large.On the other hand the slightest vibration produced by a running cockroach may elicit prey capture.Interestingly,some potential prey animals like grasshoppers sometimes pass by the spider as if unnoticed. Typically,these "vibrocryptics" move very slowly and smoothly. We have recorded vibrations produced by them and found them to be made up of only very low frequencies strongly reminiscent of background vibrations due to wind (more details in Barth et al.1988b).

(iv) *Courtship vibrations*: We have good reasons to believe that the male courtship vibrations contain the information necessary for the female to recognize the male as a conspecific. The frequencies contained in the male vibrations of the different species of the genus *Cupiennius* are largely the same. Furthermore,they are within the range of those of prey vibrations. There are obvious differences in the *temporal characteristics*,however (Barth 1986;Barth et al. in prep.). Experiments in which the female's behavioral response to synthetic male courtship signals was studied (Schüch and Barth 1986 and in prep.) have indeed
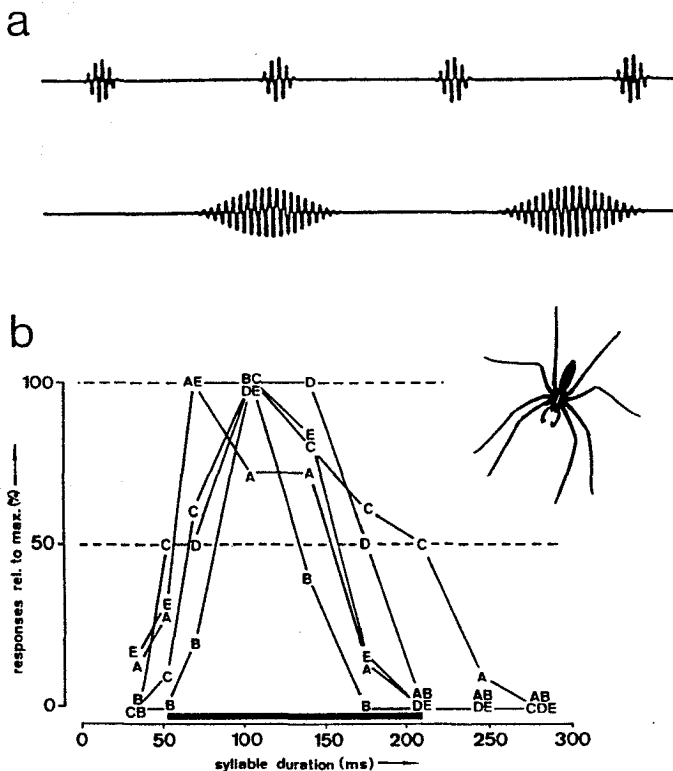
a

b

Fig.3 Synthetic male courtship vibrations (a) and female behavioral response (b),<u>C.salei</u>. The parameter varied in the given case is syllable duration. In b responses are given for 5 females (A-E) in % (100% is the number of responses to the most effective value of syllable duration). (From Schüch and Barth,in prep.)

shown that temporal parameters may vary only within very narrow limits; otherwise the female will not respond with its own vibration. The most critical temporal parameters are the duration of a syllable (fig.3) and the pause between two consecutive syllables. In conclusion, a large number of such experiments demonstrated narrow temporal filters in the female vibration sensitive system. At the same time there is a very narrow frequency filter: the female responds readily to a syllable with a carrier frequency of

ca.100Hz which is in the natural frequency range.It does not respond,however,if the carrier frequency is lower than 50Hz or higher than 210Hz (Schüch and Barth 1986 and in prep.).

Our attempt to understand the importance of vibrations in spider behavior and to elucidate the underlying physiological mechanisms has prompted experiments on a number of rather hetero- geneous aspects of spider biology: *sensory physiology*, asking for both peripheral and central nervous mechanisms; *ecology*,with such aspects as the dwelling plants,the propagation of vibrations by plants, and the physical properties of the naturally occurring signals being important issues; *ethology*, dealing with the spider's responses to different types of vibrations.The problem of courtship signal distinction and species recognition prompted *taxonomical work* (Lachmuth et al. 1985) and a study of the range distribution and sympatry of the various species (Barth et al. 1988a).

As seen from the work outlined here in short form laboratory and field work,physiology and general biology,reductionism and a more organismic view of our problem do not exclude but complement each other reminding us of the fact that all these different aspects are related to the same undivisible living being.

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Jocqué: Is the female's response to vibrations influenced by
the length of the experiment?

Barth: We use the females only once a day for the experiment to
avoid habituation effects which are obvious if one repeats the
experiment with the same animal at intervals of, for instance,
20 min. Changing the duration of a particular experiment by in-
creasing the number of vibration syllables has very little ef-
fect on the female's response. Even when exposed to 1000 syll-
ables (the average number under natural conditions is 12) the
female will not respond more often than about three times.

Munoz-Cuevas: Quelle est l'intégration du phénomène vibratoire
au niveau du système nerveux central?

Barth: The interneurons we have so far examined with regard to
their vibration sensitivity are located in the suboesophageal
nervous mass. They are clearly tuned to rather narrow frequen-
cy ranges. Their threshold curves have band pass characteris-
tics. This leads us to believe that one of the integrative
functions of vibration sensitive neurons in the CNS is to
'pick out' the frequency ranges of biological significance
from a broad spectrum of frequencies. However, the interneurons
studied are not the only ones in the CNS dealing with vibrat-
ions. There are no data available on the neurons in the brain.

Krafft: Que savez vous au sujet de la phéromone féminine
(origine, nature, spécifité) à laquelle repond le male?

Barth: Unfortunately, we know very little about the female
pheromone. A lot of research is still needed to understand
spider pheromones in general. We have done a few behavioural
experiments mainly trying to find out how species-specific the
response of the male to the threadborne pheromone(s) of the
female is. The results of these experiments show that the
'arousal'-effect of the female pheromones is rather independ-
ent of the species used (Cupiennius salei, C. getazi, C.
coccineus). In other words: the males also respond to the
pheromones of the 'wrong' female. For Cupiennius we also know
that female pheromones are not necessary for the guidance of
the male to the female. Also, mechanical guidance by a female
dragline is no necessity. We have reasons to assume that the

female vibration signal is sufficient for the orientation of
the male towards the female.

Krapf: Zur vibratorischen Krypsis (eine Heuschrecke kann unbe-
merkt an der Spinne vorbeilaufen): Warum lösen nicht Luft-
vibrationen der Beute eine Fangreaktion aus?
Barth: Vermutlich sind die Nahfeldvibrationen, die von der
Beute verursacht werden, ebenfalls so unterschwellig, daß sie
von der Spinne nicht registriert werden. Selbst Beutetiere,
die in nur 1 cm Entfernung vom Spinnentarsus entfernt laufen,
bleiben unter den geschilderten Bedingungen des sehr langsa-
men, 'sinusoidalen', transientenarmen Laufens unentdeckt.