An introduction into the study of behavior, using the example of the web-building spider.

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A 20-minute, colored, 16 mm sound film on the building of the geometric orb web and prey catching of the spider *Araneus diadematus* Cl. *(Araneae, Araneidae).*

Audience: High school and college biology classes, psychology and behavior courses, as well as lay groups can show this film as an introduction. It is intended to stimulate interest in behavior, raise questions, and organize thinking about some aspects of behavior: behavior being defined as movements of the whole organism.

Special approach: The film lets the viewers' eyes explore details as well as overall patterns of an organism's movements, and observe how such movements fit into nature's framework, helping a species to survive in its environment. Eight written titles explain general principles, applicable to any behaving organism. A minimum of spoken comments point toward characteristic details in the spider's movements, as a thread is laid or a prey is caught. It is left to the viewer or the instructor to decide in what depth he wants to use this film: to explore web-building behavior specifically or discuss behavior in general.

It may be found advantageous to show the film two or three times; this permits the audience to check preliminary observations and prove or disprove hypotheses formed on first showing. — An intentionally abrupt end to the film is usually followed by a barrage of questions, which can be answered by the instructor or through use of this folder and its reference list.

"Life on a Thread", tries to help the student memorize facts about animal behavior by linking them to the pleasure of watching the beauty of a complex rhythmic movement pattern.

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Comments to Content of Film:

The following text is subdivided, according to the film's sections, into eight parts, each of which illustrates some general principle of behavior, and each of which is introduced with a written title:

I. **Behavior is set at a time and in a place:** (2.5 min)

This section reminds the student that (1) specific behaviors occur in seasonal, circadian or other rhythms, frequently set in motion by special releasers like temperature and light; and that (2) through trial and error, natural selection, and aided by perceptual processes, behavior occurs in a territory.

Many species of spiders, like the female *Araneus diadematus* Cl. shown in this film, build a new web nearly every 24 hours at sunrise, when the silk glands are well-filled, daylight is beginning, and the temperature reaches its early morning minimum. Environmental factors like dark/light and low/high temperature ratios appear to play a role as releasers, their optimal combination producing the highest rate of web-building frequency. But even under constant temperature and light conditions, some webs are built every day, indicating the existence of circadian rhythm in the animal. Damage to the old web is not the cause for new construction. It has been observed in the laboratory that spiders systematically take down completely intact webs at the end of the day; they construct new ones, using only a few of the old structural lines. — From the point of view of a spider's survival, the existence of a new web at the beginning of a day appears to be ideally suited to its task, namely the catching of prey which flies by day and which uses light for orientation. A fresh web is invisible to a fly, and it holds the fly just long enough for the spider to catch it. Repair frequently occurs during the day, but only rarely is a new web constructed before the following morning. Less is known about spider species which build their webs in the evening, presumably to catch prey which flies by night; and even less has the timing of web-building been investigated in those spiders which take several days for the construction of a single web, and which elaborate rather than renew the existing structure.

The interested observer will find in certain areas many webs of one or several species closely together. Such accumulation seems to be due to two kinds of conditions: (a) a great number of prey and possibly relatively few predators have permitted many spiders to survive in one area, and (b) certain species appear programmed to seek out special environmental conditions like light, warm, structurally well suited areas, which are protected from wind. Species specific factors appear to be involved in web location, as indicated by the unequal distribution of various animals under carefully created laboratory gradients. Much of this has still to be explored, and the problem of web location seems an interesting one, given the high number of offspring in most web-builders (several hundred), combined with the rigid territoriality of a web: an *Araneus* spider, once it has built a web, will only rarely change its location.

II. **Some behavior unfolds undisturbed in the laboratory:** (2 min)

A student of behavior has to decide how the movements he wants to study can be observed with minimal distortion, frequently as close as possible to natural conditions. Territorial and social behavior of many, specifically the large animals, can only be observed in very large enclosures or by labelling and following animals in the field. Other behaviors like operant conditioning have been primarily observed under specifically designed "artificial" laboratory conditions. — There is good reason to believe that the pattern of web-building is the same in the laboratory as outdoors, and that even the hot, glaring lights used in movie making do not produce change in the web geometry. While web construction varies with age and size of the builder, it has not been found to be measurably influenced by experience. Spiders which had been fed all their lives long by mouth without ever being permitted to catch prey on their webs, or spiders which had been reared in narrow tubes where they could never build a web, constructed normal webs according to their age and size when given the opportunity. The web pattern showed no influence of their unusual experience. The shape of a web is relatively independent of the environment, as long as the laboratory frame is larger than the expected web, or the distance between supporting branches permits the spider to build the web full size. — Such considerations are important for the student if he wants to know how far his own laboratory observations can be generalized to all animals of the species under outdoor conditions.

III. **The study of behavior is concerned with the movements of the whole organism: speeding up the sequence of movements reveals the overall pattern (1st order):** (2 min)

The definition of behavior in the first part of this title was taken from the Encyclopedia Britannica; web-building is an illustration of behavior in keeping with that definition. The film uses a special approach in this as well as the next two sections: web-building is shown at very high as well as very low speed, to permit identification of behavioral patterns at various levels of nervous system integration. By reducing 30-60 minutes of web construction to one to two minutes, the observer becomes aware of very slow events which are normally outside his range of perception. For example, one notices the relative share which each web-building phase occupies; i.e. the time for radius and auxiliary spiral construction is relatively brief as compared to the long time required for the catching spiral. At high speed one becomes aware of the sequence of radius construction which shows alternation among different directions; an upper radius usually follows a lower one, a right one is constructed after a left. The rhythmic sequence of body turns and leg movements looks distinctly different for the scaffolding spiral (which is later removed), and the sticky spiral. One notices the laying of the sticky spiral in pendulum as well as fully circular turns; the uneven frame is filled with as large a number of spiral turns as possible. — It should be interesting to apply this technique of speeding up movements to many other behaviors, i.e. social, mating, prey searching behavior, so that slow, long-term movements are brought into our limited perceptual time scale. The type of phenomena which we observe in this section of the film are possibly those large pieces of behavior which are integrated in the central body, a small oval section at the dorsal, caudal part of the supraesophageal ganglion of *Araneus*' central nervous system. Lesions in the central body were followed by severe disintegration of the web pattern.

IV. A few simple movements form the building stones of behavior and appear again and again in each phase (3rd order): (3.2 mins)

In this part the film demonstrates the possibilities of a procedure opposite to that used in III: the very rapid, jerky movements of a leg or a part of the body of the animal are slowed greatly so that we can recognize details. Most striking are the probing movements of the two front legs, which the nearly blind animal uses to establish the position of threads already laid; i.e. a spider in the web center moves front legs from radius to radius until it has collected sufficient information on radial angles to leave an angle as is, or further subdivide it. Receptors for leg positions may be the lyriform organs which appear at joints all over the body of a spider. Elimination of one or two legs has been found to interfere only minimally with web-building, indicating that an intact leg can take over a missing leg's functions. The probing movements which can be seen very distinctly in this film appear in every part of web construction, many hundred times altogether. Similar probing movements are used in prey catching. — Another such detailed leg movement is the manipulation of thread, and the fusing of new to old thread. For this the animal uses the hind legs and the spinnerets which lie at the end of the abdomen. The viewer can discover more such building stones of behavior, as he observes the spider in the film. Regulation of movement at the level of the reflex arc or something like the command neurons of the crayfish can be discussed. We have called these movements arbitrarily "third order", in contradistinction to the "first order" web-building pattern, and the "second order", which are the subject of the following section.

V. Composite movements are repeated many times, until a phase is completed (2nd order): (1.9 mins)

Looking at radius construction at original speed, it is apparent that during this phase of web-building a relatively complex sequence of movements is used over and over again: i.e. a spider turns in the hub, probing radius spacing; it runs to the frame of the web along a radius, next to an oversized angle, laying out new thread; it fastens the radius in exact position on the frame, disconnects it, and runs back toward the hub, rolling up the old and letting out a new radius. — This procedure is repeated until all 20-30 radii are built, and no oversized angle is perceived. — Another such set of second order movements can be observed during spiral laying, and can be defined as the sum of all motions occurring from one radius-to-spiral connection to the next. Here the spider holds the radius with one hind leg and presses the sticky thread from the spinneret against the radius. It then moves on to the next radius either directly, or via the auxiliary spiral, or the frame thread, probing for distance from the last spiral turn with one of the front legs. On the new radius the spiral is fastened in the same manner as before. In a web with 25 radii and 25 spiral turns, a second order spiral-laying movement would occur about 625 times. It may be useful to discuss such sequence of movements as coded in the central nervous system more complexly (or higher) than the third order, but below the level of integration of total web-building in the central body. The normal speed of spider movement is most suitable for observation of this part of web-building behavior. The viewer might want to try at this point to analyze the relationship of third, second, and first order movements in the web-building process.

VI. Successful completion of a phase is monitored, corrections are possible: (6.2 mins)

The uninterrupted construction of a whole orb web is probably a rare occurrence in nature: waving branches, a passing bird, or another spider may interfere with the smooth sequence of thread laying. Many experiments have shown, and the survival of spiders proves, that in web-building the spider can, within limits, compensate for disturbances of the program; the behavior is flexible, and leads to a functional end product, no matter what. In this film the spider replaces a cut radius. It can do this many times if necessary. However, there is a limit to replacement, and building may proceed, leaving the radius unfinished, if it is cut once too often. — Another method of testing plasticity of behavior consists in transfering a spider in the process of construction from its own to another spider's web: the animal usually continues wherever the new structure requires. It probes for existing threads and lays whatever is necessary to complete the trap. The spider does not follow a rigid sequence of programmed motions. — The film demonstrates also, that replacement of a cut radius is unlikely to occur, once spiral construction is underway. In this instance the spider lays the spiral across the hole, not caring to replace the missing piece of radius; the outcome is a functional web.

VII. **The outcome of patterned behavior plays an important role in the survival of an organism:** (1.5 mins)

The completed orb web can be considered an excellent solution to the problem which a nearly blind earthbound animal has in catching air-borne prey. First, the eight legs via the radii which they grasp, receive signals of motion from any direction in the comparatively wide area of the web; the legs can jerk radii to test for weighty objects, which might be entangled in the periphery. Second, the spider can quickly run with its clawed feet along the dry radii in any direction. And third, the even mesh of the web intercepts — at least briefly — any flying prey which is larger than an interspace and which happens to pass the web area. In short, the finished trap forms a most advantageous extension of the perceptual range of the trapper, as well as a good medium for rapid locomotion. This makes web-building a very high priority in a spider's life, and explains its execution even under adverse circumstances. The logarithmic nature of the spiral can be explained as an economic way for the spider to measure distances and proceed on the shortest way from radius to radius. It may be a challenge for a student to think of the orb web as a compromise between various economies, i.e. labor, material, and fineness of perception and movement.

The catching of prey follows a rather rigid sequence of events: i.e. the turning of the spider toward the stimulus in the web, jerking of radii, running out toward the prey, enwrapping and biting, repairing the hole which the struggle has left in the web, and returning to the hub. Analysis of prey-catching behavior has informed us that there are alternate sequences of behavior, which are contingent on properties of the prey, and which the spider can substitute for the sequence seen in this film.

VIII. **The outcome of normal as well as abnormal behavior can be recorded and measured:** (1.0 min)

Web photography has contributed extensively to the study of building behavior. It is apparent from this film, that the spacing and fastening of the silk is the outcome of the animal's movements; the resulting pattern of threads can be regarded as a record of the spider's behavior. Measuring distances on web photographs and calculating the regularity of spacing gives information on the degree of sensory-motor coordination of the builder. The size of the web has been shown to depend on silk supply, body measures, as well as on "drive or alertness" of a spider. Calculating average mesh size permits conclusions on the prey-catching capacity of the trap. Web measures change throughout the life-time of an animal, are different for males and females, and show family and individual idiosyncrasies. Lesions in the central nervous system of a spider cause disturbed web patterns; analysis of histological damage in relation to disturbed webs permits some conclusions on location of movement-coordinating functions in the central nervous system. Because the web has high priority, some kind of web is built even by a severely disturbed animal. The complexity of the web permits so thorough an analysis, that even minor behavioral changes can be detected. Such considerations and the accidental discovery of distorted webs which had been built after the spider had received certain drugs, have led to experimentation with mainly central nervous system active substances on spiders. Characteristic patterns have been found to be related to drug-group effects (i.e. tranquilizers, central stimulants), and by comparing drug webs to webs built under other circumstances, a limited amount of information on drug-behavior interaction has been collected.

The film ends abruptly after showing a series of photographs of control as well as drugged webs. Further explanations and reports on our knowledge of drug actions in spiders and man are too voluminous and problematic to permit exploration at the end of this film. The questions which students will raise after seeing the film can be regarded as a good starting point for a course on normal as well as abnormal behavior.

Many problems connected with behavior will have to be studied in other animal species and/or man. Other questions raised in the viewer of this film can not be answered, and they will serve to indicate the limits of our knowledge. Introducing the study of behavior through this film will hopefully serve as a valuable adjunct to teaching, and stimulate rather than persuade its viewers.

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