THE SENSES OF SPIDERS.

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Introductory.

Since there is no such thing as a "typical" arthropod, it is impossible to make generalizations concerning the characteristics of these animals from any one Class. It is possible, however, to compare one Class with another, for the fact that certain groups are more closely related to one another than to other arthropods is indisputable.

So far as the structure and operation of sense organs is concerned, spiders closely resemble insects. Yet there are also some dissimilarities between the two groups. Throughout this paper the attempt will be made to compare the sensory reactions of arachnids with those of insects. In this way one may obtain more precise knowledge of the manner in which the senses of arthropods function.

I.

The Nervous System of Arachnids.

The nervous system of arachnids is highly concentrated, even in the more generalized forms, and in spiders this concentration about reaches its possible limits. The most primitive condition is probably found in scorpions (10), which exhibit distinct segmentation of the thoracic ganglion, and have some of the abdominal ganglia distinct. The distribution of nerve trunks is also less specialized in scorpions than in spiders; for, whereas in spiders those to the labrum and lateral eyes are distinct throughout their lengths, those of scorpions have a common root (9).

In true spiders it is difficult to detect segmental divisions in the nervous system, even in microscopic sections. The cerebral mass or "brain" can be distinguished from the cephalothoracic nerve mass simply because the oesophagus, which passes between them, leaves only a pair of commissures connecting them. The thoracic mass is highly concentrated, and the nervous masses of the abdomen have disappeared or fused with those of the cephalothorax; the nervous supply of the abdomen consisting of a pair of nerve trunks which ramify throughout the abdominal tissues. Each appendage is, of course, supplied through a similar fiber from that part of the ganglionic mass nearest it. The eyes are also each supplied with a definite fiber, which in this case proceeds from the cephalic ganglion (12).

There seems to be some disagreement between authorities concerning the histological structure of the nervous system of spiders. Thus Handstrom (10) states that spiders are specialized forms, lacking "globuli cells and a protocerebral bridge"; while Haller (9) insists that the globuli are much more distinct in spiders than in other arachnids! The globuli consist of groups of specialized cells which have been assumed, on purely morphological grounds evidently, to have an associative function—that is, they are shunts connecting the sensory with the motor cells. They appear to correspond roughly to the mushroom bodies of insects.

Like other arthropods, spiders have the bodies of the nerve cells (neurons) distributed in the periphery of the ganglionic mass (or masses); the core of the ganglion consisting chiefly of fibers from the cells. Also, like other arthropods, the arachnids have the sensory cells located ventrally and the motor cells dorsally.

The concentration of the nervous system of spiders is exactly what one might expect, considering the fact that these animals have no distinct head, and no visible abdominal segmentation.

II.

Sense Hairs.

All spiders possess hairs or spines, and in some species these are so numerous that the animal appears to "wear a fur coat." This is especially true of the tarantulas (Avicularoidea).

Some of these hairs are sensory (11). They greatly resemble the sensory hairs of insects, though being less specialized, they do not exhibit the variety of form found in those animals. Two distinct types are present in arachnids (18): long, movable hairs, and shorter, fixed hairs. Both Dahl (7) and McIndoo (18) state that the long hairs are especially numerous on the legs. Dahl (7, 8) considers them auditory, but it does not seem to me that he has fully demonstrated this to be the case. There can be no doubt that the hairs are very sensitive to contact; and this, for spiders, is a very important function, since many of them depend largely upon contact stimuli. Indubitably those species which regularly spin webs perceive vibrations by means of these hairs (2). One can scarcely consider such sensations auditory, although, since the distinction between felt vibrations and hearing is not great, it is often difficult to distinguish between the two.

Many observers have noticed that during courtship the movable hairs of spiders are erected.

III.

Lyriform Organs.

There is one group of sense organs peculiar to arachnids, and which are especially numerous on the bodies of spiders. These are the so-called lyriform organs or sensilla tomosa (14). They were first studied in detail by McIndoo (18), who described them as "flattened funnels, each communicating with a sense cell." Kaston (14) describes them in detail. According to him, each organ consists of a number of more or less parallel slits in the cuticular layer. The slits are separated by thick laminae, so that externally the organ somewhat resembles a grid. A thin layer of material covers the exposed surface, and a similar layer determines the inner limits of the organ. Below the cuticular part lie elongated, hypodermal cells and bipolar sense cells; one sense cell for each slit of the organ. A sensory fiber from the nerve cell traverses the slit between the membranes, which is filled with fluid.

There are single as well as compound lyriform organs. The organs are variously distributed among different species of spiders, but this distribution has no taxonomic significance. Although especially numerous on the legs and palpi, lyriform organs are found on other parts of the body.

Various functions have been assigned to the sensilla tomosa. Both McIndoo and Kaston consider them chemical sense organs.

IV.

Eyes.

The distribution of various types among arthropods is peculiar. The crustaceans have only compound eyes, the arachnids (with the exception of ticks) have only ocelli, while insects have both. With the exception of those of house centipedes (which are compound), the eyes of myriapods are aggregations of ocelli.

Fundamentally the eyes of spiders do not differ structurally from the ocelli of insects. Each consists of: 1) a corneous, transparent, and usually colorless cuticular lens; 2) hypodermal cells with their long axes perpendicular to the surface of the eye; 3) accessory pigment cells; 4) a retinal layer comprised of the terminal fibers of sense cells. Between certain of the hypodermal cells rods (rhabdomes) are situated (4). There are certain variations between the histological structures of median and lateral eyes of spiders which we need not consider here. (See Widmann, 31.) Of greater interest is the fact that the median eyes of some spiders are equipped with muscles which, by producing horizontal and vertical rotation of the organs, are capable of bringing about a certain amount of accommodation (28, 32).

The number of eyes varies in different groups of spiders. Phalangids have but two; the greatest number found in any species is eight. There is also considerable variation in the development of the eyes themselves; Lycosidae and Salticidae being better equipped in this respect than other families.

V.

Vision.

A considerable amount of study has been devoted to the vision of spiders from the morphological standpoint. Scheuring (28) has determined instrumentally that the field of binocular vision is 50° for *Tegnaria atrica* and 80° for *Salticus scenicus.* These represent two extremes. The angle of *complete* vision is as much as 170°–180°. The angle of vision is not the same in all directions, even in a single species. Phalangids have a very limited angle of binocular vision (25°), which finds some compensation in their wide angle of complete vision (200° in all directions).

By measuring the refractive indices of the lenses and the number of rhabdomes stimulated, Petrunkevitch (23) decided that the angle of vision for *Phiddipus* is 8′, for *Lycosa* 60′ and for ourselves 1′. From this he concludes: "A creeping insect about 1 sq. cm. in size would be perfectly visible to the human eye at a distance of 3 m., while it would appear as a moving speck to *Phiddipus,* and would be totally beyond the range of vision of *Lycosa.*"

Of course this is not experimental proof in the real sense. In fact there seem to have been no careful and extensive experiments made on the vision of spiders. It is quite obvious, however, even from casual observation, that visual acuity varies remarkably between different species. Thus Petrunkevitch (24) observes that *Dugesiella hentzi* does not appear to notice even "a large object (such as the hand) in motion." The Peckhams (21) insist that most of the North American Attidae can see "small, immovable insects" at a distance of five inches, that they see larger insects at even greater distance, and recognize members of the opposite sex at least a foot distant.

As one approaches the "face" of an Attid spider with the end of a pencil or other similar object the animal "rears up" by elevating the cephalothorax, and walks backward. If one moves the object to one side of her, she quickly turns to face it. Blinded Attids do not behave in this way, and in fact become quite sluggish.

Dr. Wm. Barrows informs me that he has seen a captive specimen of *Dolomedes tenebrosis* seize successively eight houseflies on the somewhat slippery surface of a table. This behavior practically rules out every sense excepting visual space perception.

VI.

Responses to Vibration.

It has long been known that spiders respond to movements of their webs, even when the object that produces the vibration cannot possibly be detected in any other manner. In fact the spider may respond in this way to objects which have absolutely no value for her. The common garden spider, *Argiope* (*Miranda*) *aurantia*, will seize the tines of a vibrating table fork touched to her web. Barrows (2) states that *Epeira sclopeteria* orients to vibrations of this kind; and noting that while the smaller specimens react to higher vibrations (100 to 480 per sec.), the larger ones respond to the lower vibrations (127 to 284 per sec.); claims this to be an adaptation of the size of the spider to that of her prey.

Both Dahl (7) and the Peckhams (22) insist that these responses indicate the presence of an auditory sense. On the other hand Lecaillon (16) points out that even the spider's ability to distinguish differences in pitch does not prove the presence of audition, since such differences may be "felt" through the web. The only indication that an auditory sense may be involved is the fact that some spiders, when deprived of webs, and resting on a solid surface, still respond to air vibrations.

Wells (29), after experimenting on a number of species of *Epeira* and *Argiope* with a tuning fork (C1 28), found that a great variety of responses were given, not all of which were positive. Some specimens, for instance, dropped from the web; others shook the web; and some changed position.

Pirata piratica lives upon the surface of water, over which it runs (27). When an insect falls into the water, the spider quickly orients to the source of the vibrations produced, and runs in that direction until it encounters its prey.

VII.

The Chemical Senses.

A number of experiments have been made to determine whether or not spiders possess olfactory and gustatory senses. The least satisfactory of these have been made with various essential oils (18, 22, 26); although the Peckhams noticed that the removal of the palpi of *Argiope riparia* interferes with responses to even these substances.

Considerable work of this kind has involved the mating reactions of spiders. Kaston (15), although he admits that certain species (*e.g., Dolomedes scriptus*) depend almost entirely upon chemical guidance in the selection of mates, believes that in such cases mechanical stimuli are also indispensable. Savory (27), although he makes no definite statement to that effect, seems to think that distance chemical stimuli are operative. He further states that spiders can locate water by the vapor which it gives off.

Bonnet (5) induced *Dolomedes* (sp.?) to accept bits of water-soaked cotton, which, however, were abandoned after a few minutes; but cotton saturated with meat juice was retained for several hours. Conversely, the spiders refused flies soaked in gasolene.

Argiope (Miranda) aurantia (1) is very sensitive to water, especially after being deprived of it for several hours. It will seize and drink from water-soaked cotton touched to any part of its body. It does not react in this way unless touched. But if a piece of cotton soaked in beef extract is brought *within 5 mm. of the palpi,* it is quickly seized. Sometimes this act follows extension of the palpi toward the substance. Moreover specimens deprived of palpi, or with those organs covered with shellac, pay no attention to the stimulus, although they sometimes move the chelicerae when it is brought near the legs. Similar reactions are exhibited by some other species.

It seems very likely that spiders do possess an olfactory sense, although this is probably neither very keen nor very well differentiated from what we generally consider gustatory. A somewhat similar condition obtains among insects.

Some spiders certainly respond to chemical stimuli from the opposite sex. Is it too much to expect such a sense to operate in the selection of food? Consider the fact that most spiders do not see nearly as well as insects, that web-builders are often deceived even by vibrations, and one is forced to suspect that the spider must at least have some means of distinguishing chemically between edible and inedible substances. This is further supported by the rejection by spiders of strong-smelling bugs and other insects.

VIII.

The Relation of the Senses to General Behavior.

We have already found that spiders are very sensitive to mechanical stimuli. Sometimes such responses take rather peculiar forms. Thus *Pholcus phalangoides,* according to Murphy (20), if touched as it hangs from a single thread, spins rapidly about for several seconds. Repeated stimulations produce a rapid increase, and then a decrease in the duration of the responses, and if continued, finally induce the spider to run away and hide. Petrunkevitch (24) states that the courting male of *Dugesiella hentzi* behaves as if "lost" the moment he loses contact with the female.

Especially curious is the behavior of the female spider toward her egg cocoon. Cocoons disguised to resemble other objects are not accepted by their owners, according to the Peckhams (21). On the other hand, spiders will acept as cocoon balls of cotton or other "fuzzy" objects. The female spider will accept the cocoon of another spider, but if she is kept from her own and all others for several days, will have nothing to do with any cocoon (17)! Odor as well as contact may influence the animal in such instances.

Chemical stimuli are certainly combined with contact in the mating of some spiders. Thus Kaston (15) was able to induce the courting reaction in *Dolomedes scriptus* simply by allowing the male to walk over a plate covered with the "washings" from a female of the same species. Mating appears to depend generally upon a combination of stimuli.

Spiders also exhibit a variety of responses to gravity, air-currents, differences in light intensity, etc. (27).

Certain generalized responses to light are exhibited by spiders. Of special interest is that observed by Montgomery (19) in the case of *Grammonota inornata,* a species living upon the seashore. If disturbed, this spider runs landward, excepting when the sun is directly overhead, at which time it may move in any direction. This is a negative response to light reflected from the water. Some spiders respond to any large object moving above them, by running in the opposite direction (27). The so-called responses of spiders to colors (22) are probably due to differential light intensity (27).

IX.

Variations in Behavior.

The spider is not a machine, in spite of the efforts of some students to define its activities on this basis (27). This is amply demonstrated by the variations in the behavior of even the same spider upon different occasions. Berland (3) found that *Nemoscolous laurae* modifies the form of its web when confined. Both Wells (30) and Porter (25) emphasize the fact that such variations are numerous and easily observed.

Variations occur especially in the making of the web, method of feeding, mating, treatment of progeny, etc. Lecaillon (17) describes some of these peculiarities of behavior in detail. If a female *Theridium lineatum* is placed in the presence of several cocoons, she will bind three or more of them together. If two females of *Chiracanthium carnifex* are placed upon one web, they will each take possession of a part of it and defend it as her territory.

Porter (25) explains these variations in behavior by saying that, although they cannot be considered intelligent, they are adaptive in the sense that those most favorable are preserved. This seems to be a very sensible conclusion.

X.

Social Spiders.

Jambunathan (13) has called attention to the social habits of *Stegodyphus sarsinorum,* a spider indigenous to southern India. A number of spiders spin a large, communal web, having a central, more compact, place of retreat; the remainder of the web serving as a snare. A large insect is often shared as food by several spiders, and several members of the colony work together to repair or extend the web. Adult females have also been observed to leave prey they had captured to their young. Males and females inhabit the web in about equal numbers, apparently amicably. During the winter the walls of the inner refuge are thickened.

An editorial note appended to the above paper states that probably all species of *Stegodyphus* are communal, and that so also is *Uloborus republicans* of tropical America.

XI.

Concluding Remarks.

This paper has exhausted neither the literature concerning, nor the experimental possibilities of the senses and behavior of spiders. Indeed one of the outstanding facts is that there is really very little known concerning the whole matter. Although less complicated in structure and less diversified in form than insects, the spiders are by no means "simple animals." There are no simple animals.

I should like to append a few problems in spider psychology that are badly in need of investigation.

1. No one, so far as I am aware, has ever made experiments to determine the reflexes associated with the different parts of the arachnid nervous system.

2. A more careful study of the exact functions of the tastile hairs should be made.

3. Careful investigation should be made of the chemical senses, especially as concerns their location and manner of operation.

4. Responses of spiders to moisture should be greatly amplified.

5. Responses to vibration require further investigation; especially the possible effect of air vibrations alone.

6. Extensive experiments should be made on responses to differential light intensity and color, with a view to discovering whether or not these are distinct reactions.

7. Apparently no one has ever tested the space perception of Lycosids, Salticids, and other spiders with better devěloped eyes.

8. Some of the more obscure phases of spider psychology are awaiting discovery through more extended experiments on the responses of spiders to their egg cocoons.

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After this paper was prepared I encountered an interesting reference which should be included. This was published by H. Blumenthal in 1935 (Ztschr. wiss. Zool., 29, pp. 667–719). The author has demonstrated on the legs and palpi of both sexes of most of the species examined, microscopic pits, each bearing a conical prominence, and communicating with a sense cell. The organs are absent in the more primitive families of spiders (*e.g.,* Filistatidae Telemidae, etc.).

Spiders possessing the organs can detect the presence of a great variety of chemical substances in extreme dilutions: for example they distinguish between water and .7 per cent solutions of sugar, salt, and saccharine. Excision of the organs eliminates the responses.