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CHEMICAL SIGNALS BOUND TO THE SILK IN SPIDER COMMUNICATION (ARACHNIDA, ARANEAE)

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ABSTRACT

The silk produced by the spider contributes not only to the security of the individual (dragline, retreat, eggsac) and to capture prey (snare) but also plays a role in the exchange of information between individuals. The structured silk constitutes a network favorable to the transmission of vibratory phenomena but a single silk thread can also inform a spider of the presence of a conspecific and of its sexual identity through tactochemical cues. A number of authors have shown, namely in Lycosidae, that the substratum of the female's silk with which a pheromone is associated, triggers off the courtship of the male. Moreover, an individual coming across a dragline can orientate its locomotion according to the identity of the spider which emitted the thread. Results obtained with *Tegenaria domestica* and *T. pagana*, in a T-maze, show that specific female sexual factors associated with the silk enable the male to orient its movements. The nature of these factors has not yet been determined. It is probably a pheromone. In our experimental conditions the specification of these factors appears to be only partial. A male coming across another species' dragline will follow it. But given a choice between a conspecific dragline and a different species' dragline, it will move towards the former. Finally, a male sexual factor able to orientate the female's direction has been demonstrated in *Tegenaria domestica.* The silk-provided tactochemical information allows the spiders to orient themselves towards conspecifics and to adjust their behavior (courtship behavior) according to the conspecifics they may meet. Similar results have been obtained with another species of Agelenidae *(Coelotes terrestris)* and with two species of Araneidae *(Araneus sclopetarius* and *A. cornutus).*

In social spiders there exists the problem of group cohesion which has been studied by using the same techniques.

INTRODUCTION

Communication obviously is necessary in social animals, but it is also needed by solitary animals, at least during courtship and in agonistic interactions (Riechert 1978). The act of communication implies the emission of a signal, its transmission and its reception. Signals transmitting information can be chemical, visual, vibratory or tactile. If it is a chemical signal, it is termed a pheromone. Chemical signal are known to be involved in spider sexual behavior (Krafft and Roland 1980), in parental care (Krafft and Horel 1980) and in cooperative behavior (Krafft 1979). Up until now, experiments in spiders have only demonstrated pheromones that are bound to the silk and to the integument, though the existence of volatile pheromones emitted by female spiders has been suggested by Bristowe and Locket (1926), Millot (1946), Blanke (1973) and Tietjen (1979).

Tactochemical stimuli are known to be important to the courtship behavior of male spiders representing a variety of spider families (Pisauridae, Bristowe 1958; Salticidae, Crane 1949, Legendre and Llineares 1970, Lycosidae, Kaston 1936, Rovner 1968, Hegdekar and Dondale 1969, Dondale and Hegdekar 1973, Richter and Stolting 1971, Dumais et al. 1973, Farley and Shear 1973, Tietjen and Rovner 1982, Filistatidae, Berland 1912, Araneidae, Blanke 1973, Locket 1926, Dictynidae, Jackson 1978). Various workers have examined the role of silk-bound pheromones in spiders (e.g. Kaston 1936, Dondale 1977). Dijkstra (1976) was the first to use a complex maze to show that males are capable of orienting preferentially to female draglines. Tietjen (1980) used a different technique to show that male lycosids follow females' draglines, something initially investigated by Engelhardt (1964).

Our laboratory has been studying the mechanisms of communication in spiders for a number of years. We have developed a technique for the study of male orientation to silk-bound pheromones: the method takes into account the particular behaviors of various spider families.

METHODS

We adapted a T-maze for use on spiders (Krafft and Roland 1979), which permits the study of sexual attraction in different species of funnel-web builders: *Tegenaria domestica* (Clerck), *T. pagana* (C. L. Koch) and *Coelotes terrestris* (Wider). It was also used to test the response of the araneid, *Araneus sclopetarius* (Clerck). This same technique also allows one to study the chemical factor that causes group cohesion in the social eresid *Stegodyphus sarasinorum* (Karsch).

Our experimental design involves observing the movement of a spider in a T-maze as a function of a stimulus previously placed in the maze. The following stimuli were used:

1 – a silk substrate produced by a spider permitted to roam freely in one arm of the maze during a 30-minute period (the other arm of the T was closed off).

2 – as in 1, but the silk is removed with a brush.

3 – a dragline extracted from an anesthetized (CO_2) spider and placed into the T-maze by the experimenter.

4 – airborne odors blown across the arm of the T-maze.

In performing these experiments, we held the environment constant while alternating the experimental arms of the T-maze, right and left. Adults were used in all experiments. Each type of experiment was repeated from 30 to 250 times, chi-square tests were applied to the data to test for significance.

RESULTS

Sexual attraction.—The results of the trials involving a test for sexual attraction are shown in table 1.

Female pheromones: when a female walks in the maze, she appears to modify the environment in a way that influences the orientation of the male (exp. 1). The male is unable to orient (exp. 2) to the female when the silk has been removed. Finally a single thread is sufficient for male orientation (exp. 3). These experiments show that the factor responsible for orientation by the male is bound to the silk.

Table 1.–Sexual attraction. In each experiment a number of individuals (ranging from 30 to 250 were given a choice between stimulus A or B in a T-maze. The significance levels obtained from Chi-Square tests are: ns = not significant, * = 0.05, ** = 0.01, *** = 0.001.

Experiment No.	Sex	Test Situation arm A	arm B	*Tegenaria domestica*	*Tegenaria pagana*	*Coelotes terrestris*	*Araneus sclopetarius*
1	♂	♀ substrate	none	***	***	***	***
2	♂	♀ substrate (silk removed)	none	ns	ns	ns	
3	♂	♀ thread	none	***	***	***	***
4	♂	♂ substrate	none	ns		ns	
5	♀	♀ substrate	none	ns	ns	ns	
6	♂	♀ substrate	♂ substrate	***		***	***
7	♂	heterosp. ♀ thread	none	**	**		***
8	♂	conspec. ♀ thread	heterosp. ♂ thread	***	***	***	**
9	♀	♂ substrate	none	***		*	

It is reasonable to assume that the orientation factor is a pheromone. Preliminary observations made with a scanning electron microscope showed no differences in texture among silk from male and female *Tegenaria domestica, T. pagana* and *Coelotes terrestris.*

Males do not show a corresponding orientation to a male substrate (exp. 4) and females do not respond to female substrate (exp. 5). Given a choice between male and female substrates, males further orient only to the female substrate (exp. 6).

These individuals do not respond simply to conspecific silk, as is known for social spiders (see below). Males only show the orientation response to female silk.

To determine whether the latter response is species-specific, a choice was offered between no silk in one arm and female silk of another species of the same family in the other arm (exp 7). The results suggest an absence of specificity in the female sex pheromone. However, given a choice between silk from a conspecific female and from heterospecific female, the male shows a preference for his own species (exp. 8).

Male pheromone: Until recently, there was a tendency to view sexual behavior in spiders rather rigidly–the male has an active role and the female has a passive role. Lately, a number of observations have indicated that there is an exchange of information between the partners (Platnick 1971, Krafft and Leborgne 1980). Certain facts suggest that males produce a chemical signal for the females and even for other males. According to Ross and Smith (1979), the male's silk in *Latrodectus hesperus* causes a sexual response in the female. Tietjen (1979) supports that males of *Lycosa rabida* may emit an airborne pheromone that modifies the behavior of other males. In our own studies, evidence suggests that the female orients towards a male substrate in *Tegenaria domestica* and *Coelotes terrestris* (exp. 9).

Social attraction.–In social spiders there exists the problem of group cohesion. By using the same techniques as before, we obtained the results seen in table 2.

Social attraction does not depend on an olfactory stimulus in *Agelena consociata* nor in *Stegodyphus sarasinorum* (exp. 1 and 2).

In contrast, the silk of adult female *S. sarasinorum* provides a social cue that stimulates the orientation and the aggregation of conspecific of the same sex (exp. 3). Aggregation is not observed when the silk is removed (exp. 4). The stimulus is bound to the thread. That

Table 2.– Social attraction. In each experiment females of two species of social spiders *(Agelena consociata* and *Stegodyphus sarasinorum)* were given a choice between stimulus A or B in a T-maze. The significance levels obtained from Chi-Square tests are: ns = not significant, * = 0.05, ** = 0.01, *** = 0.001.

Experiment No.	Species	Test Situation arm A	arm B	Chi-Square results
1	*Agelena*	odor of 5 spiders	none	ns
2	*Stegodyphus*	odor of 5 spiders	none	ns
3	*Stegodyphus*	*Stegodyphus* track	none	***
4	*Stegodyphus*	*Stegodyphus* track, silk removed	none	ns
5	*Stegodyphus*	*Stegodyphus* thread	none	***
6	*Stegodyphus*	*Araneus* thread	none	*
7	*Stegodyphus*	*Stegodyphus* thread	*Araneus* thread	**
8	*Stegodyphus*	*Stegodyphus* thread	*Amaurobius* thread	ns
9	*Stegodyphus*	*Stegodyphus* thread	*Eresus* thread	ns
10	*Stegodyphus*	*Stegodyphus* thread	*Amaurobius* and *Eresus* threads	*

is, the thread alone is sufficient for the response, as shown in exp. 5, in which we placed a thread from a female into the maze. However, the response may not be species-specific entirely, since, when faced with a choice between silk from *Araneus* and no silk, females selected the *Araneus* silk arm (exp. 6). Female *Stegodyphus sarasinorum* did prefer conspecific silk when offered a choice between that and the silk of *Araneus* (exp. 7). When the choice is between conspecific silk and that of other cribellate spiders *(Amaurobius* and *Eresus),* female *Stegodyphus* had greater difficulty in making the distinction (exp. 8-9 and 10). It appears that draglines of all of these species contain each a part of information that intervene in the orientation of *Stegodyphus.*

DISCUSSION

The results obtained with different species of agelenids and araneids show that males are able to orient to female threads. This orientation depends on a chemical factor that is bound to the silk and which is likely a female sex pheromone.

Several questions still exist. First, in addition to mere detection of the chemical, there may be directional information based on the physical nature of the thread, as was suggested by Tietjen (1977). Next, there is the possibility of the breakdown of the pheromone after a more or less lengthy delay. This could transmit temporal information to the male. If the pheromone is short-lived, the detection of an active thread of a female by the male would indicate that a female is in the immediate vicinity. In lycosids, the pheromone is known to be broken down by moisture such as dew. This was shown by Hegdekar and Dondale (1969), Dondale and Hegdekar (1973), and Gwinner-Hanke (1970). For spiders dwelling in protected habitats, such as *Tegenaria domestica* and *T. pagana* some other mechanism would have to operate. Finally, there is an increased possibility of female location by the males of these web species, if the female leaves the web, thereby providing threads that extend some distance away from the web. Except for the observations by Riechert on *Agelenopsis* (1981) little information exists on the degree of activity exhibited off the web by web spiders.

In *Tegenaria*, we showed that enough specificity exists in the chemical properties of the silk to provide an interspecific barrier. Although under laboratory conditions, the male may follow the thread of a heterospecific female when no other thread is available, he selects a conspecific thread when offered a choice between threads. Perhaps there is common chemical information on the silk among related species. However, isolation and analysis of the pheromone is necessary to determine this. In the sympatric species *Tegenaria domestica* and *T. pagana*, the relative specificity of the pheromone plays an important role in reducing the risk of interspecific encounters. However, in case of an error, vibratory communication between male and female spiders serves as a second mechanism to reinforce the interspecific barrier. (Krafft and Leborgne 1980).

Location of the female is not the only function provided of the pheromone. Males of certain species begin courtship behavior in response to the female's silk, as shown long ago by Bristowe (1926) and others. One can imagine that the effects of chemical stimulation in the male that has contacted female silk could modify the responsive state of the male to yield a selective sensory condition that prepares him to react positively to new stimuli emanating from the female.

As to the social spiders, the information contained in the silk has a very different function in contributing to group cohesion, particularly in keeping the individuals of the society in the nest (Jackson 1978). It is clear from these findings and ideas that silk is important in spider communication, in that it provides the basis for chemical information as well as acting as the carrier of vibratory communication.

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