

# Preliminary electrophysiological study of the contact chemoreceptors in a spider

## *Étude préliminaire électrophysiologique des récepteurs de contact des araignées*

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(Received 13 November 1997, accepted after revision 21 April 1998)

**Abstract** – During the first stages of their life, young spiders of the species *Tegenaria atrica*, show behavioural changes that lead them from eusocial groups (5–20 days old) to a solitary life (40 days old). This change is paralleled by an increase in their number of contact chemoreceptors, previously shown to be used during social interactions. We have examined whether these chemoreceptors exhibit functional changes using morphological and electrophysiological techniques. Our results indicate that such changes do not occur at the level of the chemoreceptors, thus suggesting that this behavioural shift has another physiological ground. (© Académie des sciences / Elsevier, Paris.)

spider / gustative chemoreceptors / morphology / electrophysiology / *Tegenaria atrica* / Araneae / Agelenidae

**Résumé** – Au cours de leur développement, les jeunes araignées de l'espèce *Tegenaria atrica* passent d'une phase asexuée grégaire (5 et 20 j) à un comportement solitaire (40 j). Cette modification comportementale s'accompagne d'une augmentation du nombre de sensilles chimioréceptrices impliquées dans les interactions sociales. Nous avons examiné par des techniques morphologiques et électrophysiologiques si cette modification comportementale pourrait être liée à une modification de la physiologie des sensilles gustatives des tarsi. Les résultats obtenus suggèrent que l'équipement sensoriel n'est pas modifié au cours du développement. (© Académie des sciences / Elsevier, Paris.)

araignée / chimiorécepteurs gustatifs / morphologie / électrophysiologie / *Tegenaria atrica* / Araneae / Agelenidae

### Version abrégée

Plusieurs études comportementales suggèrent la présence chez les araignées de substances chimiques cuticulaires capables d'inhiber les tendances agressives entre les membres d'une même espèce et de prévenir le cannibalisme. Ces substances agissent comme des phéromones incitatrices identi-

fiées lors des contacts corporels. Ces phéromones sont vraisemblablement perçues par des chimiorécepteurs de contact, localisés à l'extrémité des tarsi ou des pédipalpes. Chez *Tegenaria atrica*, araignée solitaire, les jeunes vivent un mois en groupe sur la toile maternelle avant de se disperser et commencer une vie solitaire. Pendant la phase grégaire le cannibalisme entre les jeunes apparaît 4 à 5 j avant la dis-

Note communicated by Pierre Buser

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persion. Après dispersion, tous les individus passent du statut de congénère au statut de proie potentielle. Nous avons voulu voir s'il existait des différences morphologiques et de sensibilité au niveau des chimiorécepteurs gustatifs au cours du développement.

Des chimiorécepteurs de contact sont particulièrement présents au niveau des pattes et plus particulièrement sur le pré-tarse et le tarse. Ces sensilles sont caractérisées par une forme en S et un angle d'insertion important (20–30°). Le pore est positionné à l'extrémité de la sensille. Bien que le nombre de ces chimiorécepteurs augmente avec l'âge des jeunes, leur morphologie et leur densité ne varie pas au cours du développement. Des réponses électrophysiologiques sont observées chez les jeunes grégaires de 5 et 20 j. La sensibilité de ces récepteurs aux différents produits testés (sels, sucre, acides aminés) ne varie pas significativement entre les

femelles adultes et des jeunes de 20 j, sauf pour un acide aminé (L-proline). Comme d'autres espèces d'araignées, *Tegenaria atrica* montrent une sensibilité plus importante aux ions potassiques qu'aux ions sodiques. Les réponses à ces substances affectent généralement plusieurs neurones dans chaque sensille comme le montrent la forme des potentiels d'action enregistrés. Chaque sensille possède en outre un mécanorécepteur, stimulé par des mouvements latéraux de la sensille.

Chez *Tegenaria atrica*, les résultats d'électrophysiologie montrent qu'il n'y a pas de modifications de la sensibilité des chimiorécepteurs de contact aux produits chimiques testés. Des bioessais sont maintenant nécessaires au niveau de ces sensilles pour déterminer l'action des produits cuticulaires identifiés chez les jeunes araignées au cours du développement en relation avec le comportement agonistique.

## 1. Introduction

Spiders are reputed to be individualists and extremely asocial, but certain are communal. In such groups, spiders must be able to distinguish between members of their own group and others. This is a real problem during the capture of prey, because the attacking spiders have to decide instantly whether they should bite or not [1, 2]. It is possible to motivate individual spiders to attack a lure attached to a vibrator. When the vibrator moves, spiders orient and shift towards it [3]. Spiders will bite the lure if it is a prey, but never if it is a member of the society. Before engaging in a killing bite, spiders touch the prey with their first pair of legs. This contact allows them to identify the lure as a prey or as a conspecific. Contact chemoreceptors situated in the distal part of the first pair of legs seem thus to play a key role in discriminating between prey and conspecifics in the spider community.

Available data about these sensilla are scarce. Foelix [4] identified curved, blunt-tipped hairs on the legs of spiders, which he presumed to be gustatory chemoreceptors based upon comparison with those found on insect antennae. These hairs were later demonstrated to be gustatory chemoreceptors by electrophysiological recordings [5]. In spiders, contact chemoreceptors are important in sexual recognition [6–8], but few data are available on the chemical cues used in social recognition by spiders.

*Tegenaria atrica* represents an interesting step in the evolution to social behaviour in spiders. Adults remain solitary, but young spiders live in subsocial groups in the close vicinity of their mother. The mechanisms that control the female's tolerance for the young spiders on their web are not clearly established. Trabalon et al. [9] have shown that the maternal tolerance period is short and clearly limited in time. In fact this period corresponds to the gregarious phase in the developmental cycle of the young, just before dispersal. After dispersal, young spiders

live isolated from each other on their own webs. At this time, cannibalism occurs frequently and spiderlings change from conspecific status to prey status. Such social behaviour shifts linked to the development could be induced by changes in the chemical composition of the cuticle [9].

Behavioural changes induced by sensitivity modulation of contact chemoreceptors have been documented in a number of insects [10]. This can be experimentally tested by means of electrophysiological methods. According to such an hypothesis, the low behavioural reactivity of the spiders observed during their gregarious period [9], should be associated with a low sensitivity towards general food stimulants such as chemicals like amino acids and salts found in the blood of insect prey. Changes in aggressive behaviour should likewise be linked to modifications in the perception of releaser pheromones inhibiting aggressive behaviours. We aimed at testing this hypothesis by recording the electrophysiological responses of tarsal chemoreceptors from spiders at different ages, stimulated with aqueous solutions of chemicals such as salts and amino acids. Morphological observations were undertaken to support the electrophysiological work and to locate the chemosensory hairs, not yet described in *Tegenaria*. Alternately, the perception could undergo changes at the periphery and/or at higher levels of the central nervous system integration. In this work, we have considered the periphery change hypothesis because it is more amenable to experimental analysis.

## 2. Materials and methods

### 2.1. Animals

Five generations of spiders, *Tegenaria atrica* Koch, were reared in the laboratory at  $20 \pm 1$  °C under a L/D, 12:12

photoperiod. They were regularly fed *Gryllus bimaculatus* (Orthoptera) and water.

## 2.2. Scanning electron microscopy

Legs from the young unsexed spiders 5, 20 and 40 d post-emergence (six spiders/age) and from six adult females were removed and dehydrated with ethanol (sequentially with 50, 70, 90 and 100 %) and propylene oxide, and then desiccated during 1 night. They were fixed on an aluminium support, covered with gold (0.2  $\mu\text{m}$ ), and observed on Hitachi 2500LB scanning electron microscope at 10–15 KV.

## 2.3. Electrophysiological procedures

Young of 5 and 20 days old, and adult females were immobilized on a carved piece of polystyrene by means of strips of adhesive tape. The first pair of legs was disposed so that its ventral part was exposed upwards. The preparation was then mounted on a magnetic ball-joint and properly oriented under the microscope (Wild M10, Leica, Germany). A fine-tip capillary electrode serving as indifferent electrode, containing 0.01 M KCl, was inserted close to the recording site, either between the claws or in the flexible cuticle of a nearby articulation joint. Recording electrodes were filled with different concentrations of the test substances in solution within 0.001 M KCl. Electrical potentials were recorded via an Ag/AgCl wire making contact with this solution, and connected to the probe of a programmable amplifier (probe: AI 401; amplifier CyberAmp 320; Axon Instruments, USA). These signals were amplified 1 000 times, filtered with pass-band Bessel filters (lower  $f_c = \text{DC} - 100 \text{ Hz}$ ; higher  $f_c = 3\,000 \text{ Hz}$ ) and recorded as digital files on a personal computer using an analogue/digital conversion board (DT2821, Data Translation, USA; sampling frequency: 10 kHz, precision 12 bits). Data acquisition and recording were performed with a custom DOS program (ATLSPK) [11]. Recording was triggered by the initial contact that induces a large shift in potential. In addition, some recordings were performed with a DC amplifier probe designed to compensate for this electrical artefact (TastePROBE) [12].

During experiments, the tip of the recording electrode was regularly cleared by wiping with a filter paper to prevent the solution from becoming concentrated as a result of evaporation. For stimulation, the tip of the electrode was slipped over the tip of a contact chemoreceptor according to the methods of Hodgson et al. [13]. Each stimulation lasted 1–5 s and the hair was left to recover for at least 1 min before the next took place. The same electrode was used to stimulate hairs that were properly oriented and within the field of observation on a given preparation. Pure chemicals including salts, sugars and amino acids (see Results), originated from commercially available sources, were used.

## 2.4. Data analysis

Spikes were detected and sorted by software procedures [14]. Recorded signals were software-filtered with a low-pass derivative algorithm [11]. A threshold was adjusted across this filtered signal at about two times the standard deviation computed over filtered data. Given the variable shape of the spikes (see below), this threshold was set either over the mean or below. Each time the filtered signal crossed that threshold, 60 points (starting 10 points before the detection point) were extracted from the original data and stored in a spike file together with the occurrence time. These waveforms were then sorted to discard artefacts and eventually sorted by amplitude into classes [14]. The number of detected spikes during the first second of the recordings were exported as ASCII data to Excel datasheets. Statistical analyses were carried out using ANOVA and Kruskal and Wallis tests. Normality of the functions were assessed with Student *t*-test.

## 3. Results

### 3.1. General morphology and distribution of the gustatory chemoreceptors

*T. atrica* has a large number of hairs on all appendages. Contact chemoreceptors were identified on the basis of their electrophysiological responses (see section below) which correlated well with morphological characteristics. They are preferentially situated on the internal face and sides of the leg, but are scarce on the external face. Their length increases during development (5 days old:  $39 \pm 1 \mu\text{m}$ ; 20 days old:  $54 \pm 2 \mu\text{m}$ ; 40 days old:  $94 \pm 5 \mu\text{m}$ ). Their shape is similar in young and adults: their tip is directed towards the distal part of the leg; they are inserted in a slightly elevated socket (about 7.5  $\mu\text{m}$  high; diameter: 5  $\mu\text{m}$ ). Contact chemoreceptors are easily differentiated from other hairs, because they insert at a much steeper angle in the cuticle and they have a characteristic S-shape [15]. Moreover, they are translucent. Contact chemoreceptors situated near the pretarsus are similar and surround the claws. On the tarsus, metatarsus and tibia chemoreceptors are lined up in rows. On the patella and femur, they are not organized in any recognizable pattern. The surface of the gustatory chemoreceptor is covered with spines to within a few micrometres of the tips. The apical part is slight, smooth and curved in towards the spiders body. A pore is situated on this part below a spur. The size and the shape of the spur are highly variable.

In spite of the frequent use of the 1st legs for environmental recognition during spider movement, the total number of gustatory chemoreceptors is statistically equivalent on all the legs from young 5, 20 and 40 days post-emergence (table 1). The total number of gustatory chemoreceptors per leg increases with age, but the density remains the same. The distribution of the chemoreceptors

**Table 1.** Average number  $\pm$  standard deviation of gustative chemoreceptors per  $\text{mm}^2$ .

	5 days old	20 days old	40 days old
Pre-tarsus	1 352 $\pm$ 254	947 $\pm$ 99	772 $\pm$ 162
Tarsus	273 $\pm$ 19	385 $\pm$ 19	268 $\pm$ 28
Metatarsus	192 $\pm$ 13	255 $\pm$ 10	209 $\pm$ 15
Tibia	139 $\pm$ 10	183 $\pm$ 9	178 $\pm$ 9
Patella	131 $\pm$ 13	178 $\pm$ 9	164 $\pm$ 11
Femur	106 $\pm$ 6	132 $\pm$ 4	113 $\pm$ 9
Total number per leg	363 $\pm$ 56	347 $\pm$ 29	284 $\pm$ 33

Data are calculated from six spiders per age.

is identical on all legs; the density is high on the tarsus and decreases towards the femur. The density is higher on the pretarsus compared with the other segments of the leg (1 200 per  $\text{mm}^2$  versus 170 per  $\text{mm}^2$ ). The pretarsus seems to be a specialized organ for detecting the spiders' chemical environment.

### 3.2. Electrophysiological observations on contact chemoreceptors

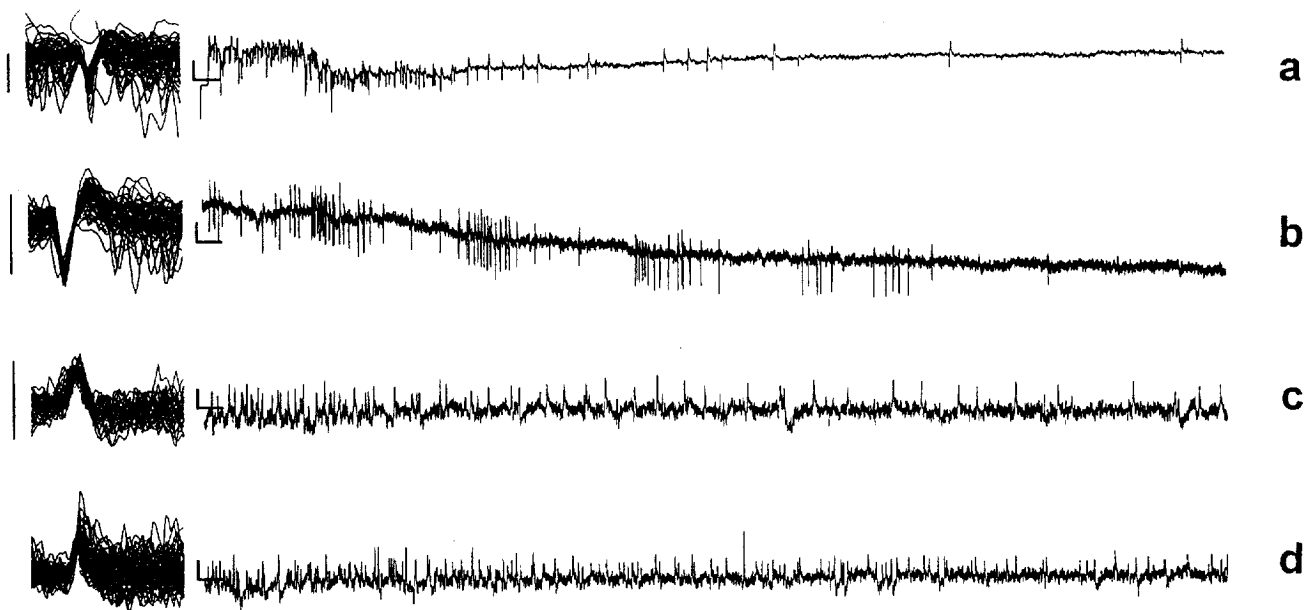
#### 3.2.1. Dose-dependent study with KCl

Spikes recorded with minimal filtering (with the TastePROBE: DC-3000 Hz) on hairs stimulated with KCl 0.1 M exhibited an amplitude of 0.2–1 mV. Spike shapes were generally biphasic, with an initial fast downward phase

(0.3–0.5 mV) followed by a slower return to baseline with a large overshoot (figure 1a, b). The total duration of the spikes was 2–3 ms. In most records, the presentation of a chemical stimulus activated more than one sensory neurone. This observation is supported by the frequent occurrence of spikes superimposed at variable delays, i.e. occurring even during the refractory phase of an individual neurone, and by the presence of different shapes of spikes as evidenced when the detected waveforms within a given record are superposed (figure 1a).

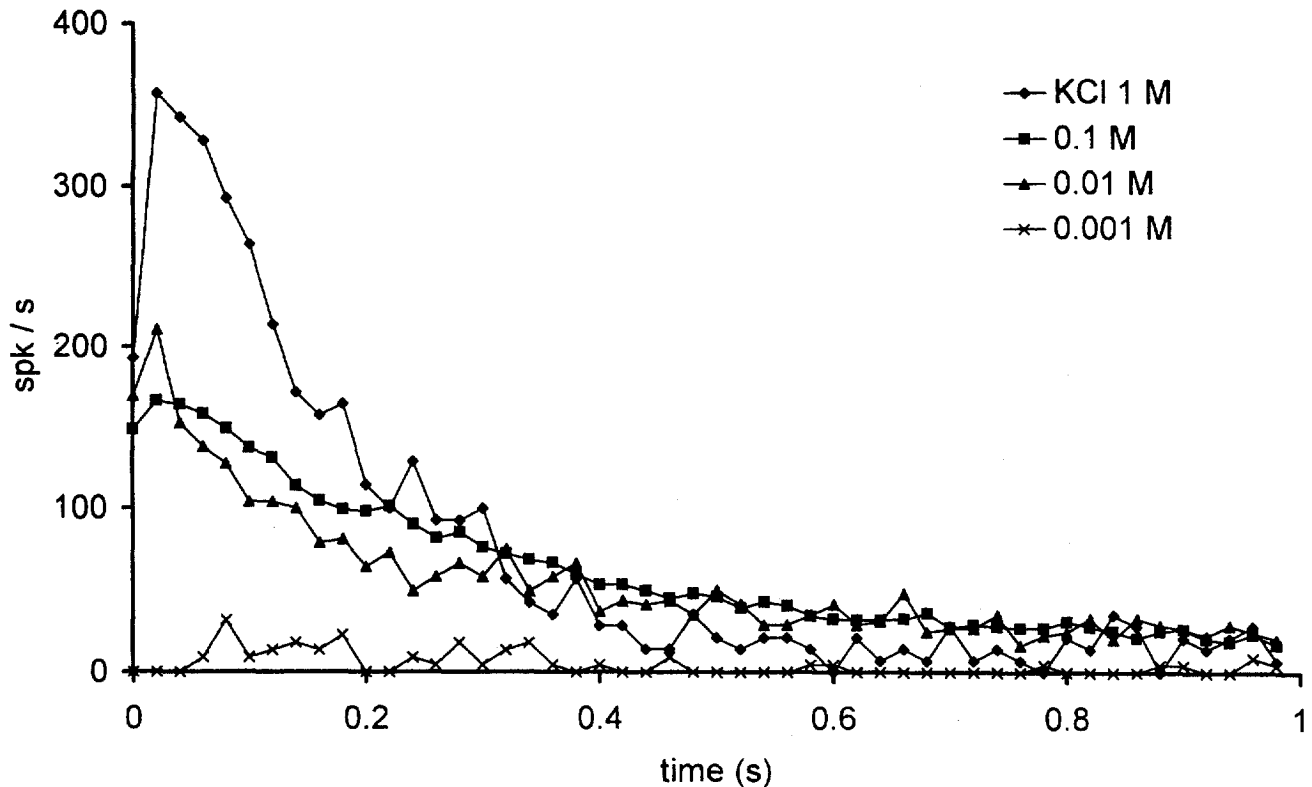
On bending, for example by imposing alternating movements to the electrode with the micromanipulator, spikes were elicited. These spikes had about the same amplitude as those observed in the presence of KCl (figure 1b). Given these observations, care was taken not to bend the hair when the stimulating electrode was brought into contact with the tip. Considering the difficulties to sort spikes according to amplitude criteria in these recordings, data were analysed as compound recordings, i.e. all detected spikes were added, irrespective of their amplitude or shape.

For most contact chemoreceptors, KCl was a good stimulant, which elicited spikes in relation to the concentration (figure 2). KCl 0.01 M was chosen as a standard to check the state of responsiveness of a given hair and was included in all stimulus series. Since KCl 0.001 M did not elicit many spikes, this electrolyte concentration was used as conductive solution for all other stimulus chemicals. As



**Figure 1.** Sample recordings from gustatory chemoreceptors of *Tegenaria atrica* legs.

Simuli: a) KCl 0.1 M; b) mechanoreceptor stimulated (bursts) by alternating movements of the recording electrode filled with KCl 0.01 M; c) saccharose 0.01 M; d) L-proline 0.01 M. Central part of the figure: first 500 ms of the original recordings (except for b: 1–3 s); horizontal bar: 100 ms (except for b: 300 ms), vertical bar: 465  $\mu\text{V}$ . The spikes detected in these records are displayed in the left column (duration 6 ms, vertical bar: 1 mV). Recordings (a and b) were obtained with TastePROBE, while (c and d) traces were recorded from inverted signals amplified with a general purpose differential amplifier (see Materials and methods).



**Figure 2.** Mean response profile of gustatory hairs stimulated with KCl at different concentrations: 1 M ( $n = 7$ ), 0.1 M ( $n = 110$ ), 0.01 M ( $n = 24$ ), 0.001 M ( $n = 11$ ).

noted before, the response was multicellular, i.e. included 2–3 classes of spikes, as judged by their amplitudes and shapes. The responses were mostly phasic; after an initial burst of potentials, the firing rate of the neurones decreased to a lower base level (figures 1a and 2). This parameter was not further analysed in the recordings. During pilot experiments with repeated and long stimulations (5 s), we observed that hairs became slack; the loss of rigidity was paired with a loss of responsiveness. Accordingly, we limited the number of stimulations on each hair up to five stimulations of 3 s in duration, separated by 1 min rest. Similar responses to these compounds were observed in 5- and 20-day-old and adult female spiders.

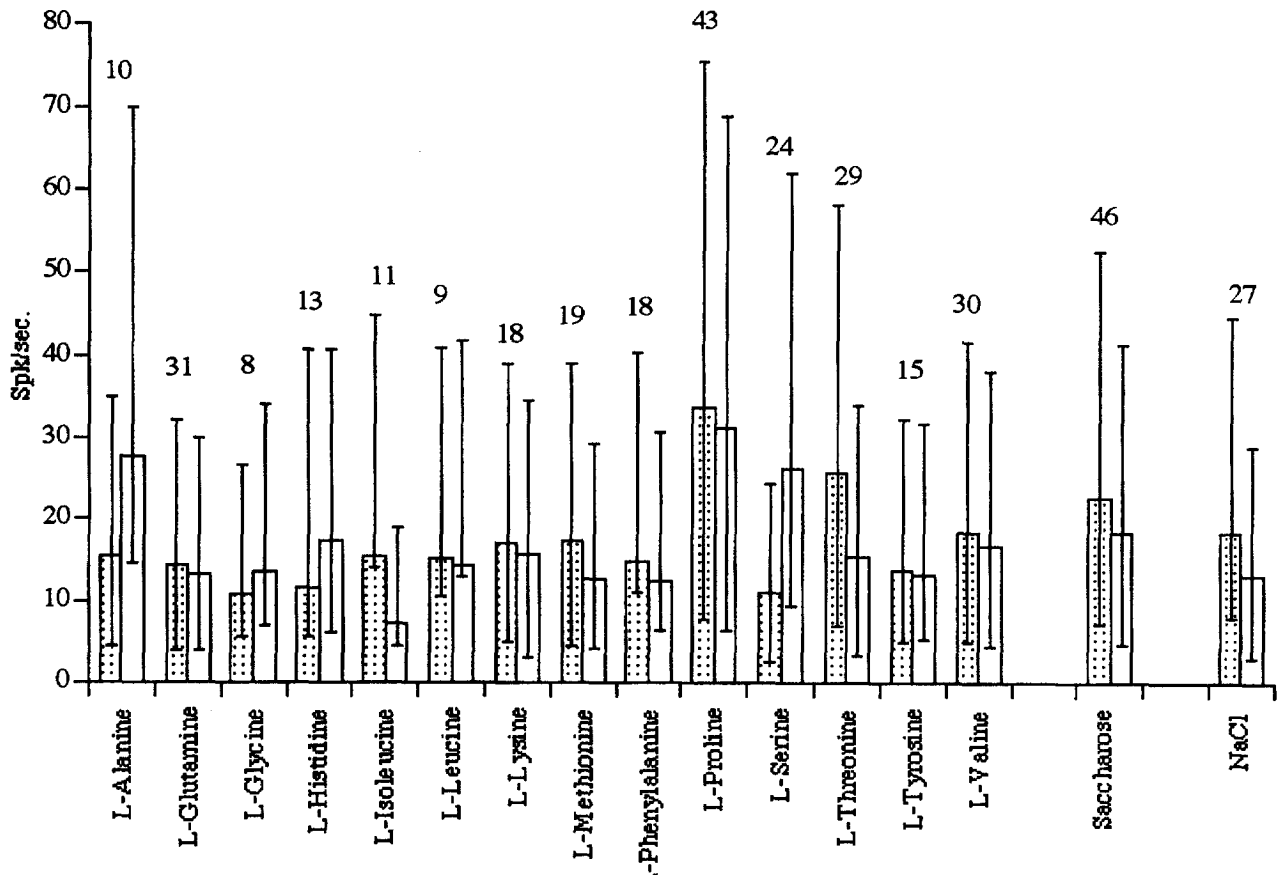
### 3.2.2. Sensibility of chemoreceptors with various chemicals

Recordings were obtained from taste receptors located on the pretarsus and tarsus. The sensitivity of chemoreceptors from female adults and young 20-day-old spiders were tested across a range of chemicals presented at 0.01 M in 0.001 M NaCl, saccharose and amino acids (L-proline, L-serine, L-lysine, L-methionine, L-phenylalanine, L-valine, L-tyrosine, L-threonine, L-isoleucine, L-glutamine, L-glycine, L-histidine, L-alanine) which were thought to be present within prey. Proline was the most stimulating compound of the series (figure 3). We did not

notice any difference between young and adults in the sensitivity to any of the substances tested. Individual chemoreceptors could present a variable response to the test substance, but at least one chemoreceptor on each spider gave a response to all of the substances tested. We compared the number of action potentials during the first second of stimulation induced by each different amino acid. This number was statistically equivalent for all amino acids except L-proline.

## 4. Discussion

In this work, we have evaluated the contact chemosensory system of *T. atrica*. Contact chemoreceptors were found on the legs and on the pedipalps, and their sensitivity was evaluated towards a set of test chemicals. The experiments indicated that extracellularly recorded responses were generally multicellular, and that some of these neurones were sensitive to salts, sugars and amino acids. Recordings performed on 5-day-old spiders indicate that contact chemoreceptors respond to the same range of chemicals as adults. These results and anatomical observations on the morphology and distribution of these receptors suggest that the peripheral sensory system is not subjected to strong modifications as postulated from the behavioural observations.



**Figure 3.** Average responses to selected salts, sugar and amino acids from adults (dots) and young of 20 days old (white).

The responses were measured by counting the number of spikes detected during the first second of each recording. Bars = average response + confidence intervals (90 % select distribution). Numbers indicate the number of observations.

Spider contact chemoreceptors share a common organization pattern with insects, but differ from them in a number of respects. Contact chemoreceptors on the body are elongated and possess a pore at the tip that lets outside molecules diffuse inside the hair and to the dendrites of the sensory neurones. Whereas insect contact chemoreceptors usually include four chemosensitive neurones and one mechanoreceptor [16, 17], spider contact chemoreceptors were reported to include up to 19 chemosensitive and two mechanosensitive neurones [18, 19]. Their morphology and external appearance are identical to those described in *Lycosidae* [4, 20]. They present a characteristic S-shape and a high angle with the leg axis. Other gustatory chemoreceptors with a smooth external cuticular have been described in *Araneidae* [4, 5]. Their external morphology in *T. atrica* does not vary between young and adults except that their size increases with age.

Contact chemoreceptor responses were found to be multicellular as in insects, but with a greater number of active units. In addition to chemosensory neurones, responses from mechanoreceptors were observed when the chemosensory hairs were deflected. Such a situation is a

general feature in insects [21] and was described also in spiders both with anatomical and electrophysiological observations [4, 5]. As the spikes elicited in these receptors were not easily differentiated from the activity of chemosensitive neurones, we took care to stimulate the chemoreceptor properly. Although the size of *T. atrica* hairs is conspicuous, they were found to be unexpectedly sensitive to repeated stimulations as if the electrolyte used within the electrode had an adverse effect on the cuticle and the nervous structures located inside the hair. This effect was avoided by limiting the number of stimuli presented to a given sensilla, but more systematic experiments are needed to tackle this problem by designing an electrolyte with the proper osmolarity or ionic composition. The second limitation encountered when recording from these chemoreceptors lies in the number of active units, which makes proper spike sorting impossible. Therefore, all electrophysiological responses concern the activation of groups of sensory neurones from which the individual sensitivity spectra remain unknown.

In spite of an increase in the number of chemoreceptors with age, their density was found to be constant during

development. These chemoreceptors are situated preferentially on the distal part of the leg (pretarsus and tarsus). When spiders move or come into contact with a substrate, these gustatory chemoreceptors are likely to play a crucial role in the analysis of the chemical environment. The gustatory chemoreceptors are functional immediately after spiders leave the cocoon. No difference in sensitivity to all the substances tested was observed between young and females adults. The average number of action potentials developed by the chemoreceptor developed in response to the amino acids tested was identical except with L-proline. As shown by Harris and Mill [5] in *Amaurobius ferox* and *A. similis*, *T. atrica* chemoreceptors are more sensitive to potassium ions than to sodium ions.

**Acknowledgments:** We thank J. Couturier for animal maintenance. We also thank Dr C. Descoins from the Institut national de recherche agronomique for his support of our work.

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## 5. Conclusion

A number of behavioural observations on spiders suggest that chemical compounds located on the spider's body are able to inhibit aggressive behaviour between conspecifics and prevent cannibalism [1, 3, 9]. These substances act as releaser pheromones and are identified by the spider after contact with another spider. The gustatory chemoreceptors described in this paper are likely to be involved in the detection of these substances. The electrophysiological results show no change in gustatory chemoreceptor sensibility to the various chemical tested. Further bioassays should be undertaken to indicate the action of the cuticular substances on spider agonistic behaviour.