J. Exp. Biol. (1970), 53, 165–169
With 1 plate
Printed in Great Britain

THE CENTRAL COURSE OF THE HAIR AFFERENTS AND THE PATTERN OF CONTRALATERAL ACTIVATION IN THE CENTRAL NERVOUS SYSTEM OF THE SCORPION, *HETEROMETRUS FULVIPES*

BY P. SANJEEVA-REDDY* AND KANDULA PAMPAPATHI RAO†
Dept. of Zoology, Sri Venkateswara University, Tirupati (A.P.), India

(*Received* 17 *March* 1970)

INTRODUCTION

There is a considerable amount of information on the central representation of the sensory input from the hairs in insects (Pumphrey & Rawdon-Smith, 1937; Fielden, 1960*b*; Rowell, 1961; Fielden & Hughes, 1962; Mill, 1963) and crustaceans (Prosser, 1935*a*, *b*, 1937; Wiersma, Ripley & Christensen, 1955; Fielden, 1960*a*; Hughes & Wiersma, 1960; Wiersma & Hughes, 1961; Wiersma & Bush, 1963). To date, no such studies have been reported on the arachnid central nervous system. This dearth of knowledge precludes fruitful comparison between the major classes of arthropods. Furthermore, in most of the studies mentioned above the emphasis has been more upon the reaction patterns and mapping of the peripheral fields of the interneurones. Attempts have never been made to label the hairs in the periphery and systematically map the central spread of the sensory fibres associated with them. The ipsi- and contralateral central discharges following the stimulation of a single hair have never been simultaneously monitored. Hence the available evidence is inadequate to explain whether the contralateral central representation of the tactile input in insects (Roeder, 1948) and crustaceans (Wiersma & Bush, 1963) is due to the terminal branches of the sensory neurones only or whether collaterals of the sensory axons passing 'through' a ganglion also participate. This point needs clarification since it is known that some of the hair afferents pass 'through' one or more central ganglia before terminating in the central nervous system (Horridge, 1968). With this in mind the hairs on the metasoma of the scorpion were 'labelled' and the central course of the hair afferents as well as the mechanisms of contralateral activation were studied in great detail (Sanjeeva-Reddy, 1969). The present paper represents a preliminary account of the results obtained and shows that the collaterals also take part in the contralateral activation. It also illustrates the suitability of the scorpion preparation for studies on the central representation of the tactile input.

MATERIAL AND METHODS

The scorpions were locally obtained and were maintained in the laboratory on a diet of cockroaches. For purposes of experimentation the animals were confined to a

* DAE (Bombay) Senior Research Fellow.
† Present address: Department of Zoology, Bangalore University, Bangalore-1, India.

wooden dissection board, ventral side up, and the nerves were exposed by carefully excising the sternal part of the exoskeleton. Scorpion Ringer (Padmanabhanaidu, 1967) was used to moisten the nerves. Silver–silver chloride electrodes were used for extracellular recording purposes. Impulses were led to Grass P9 a.c. pre-amplifiers and then finally displayed on Tektronix type 502 A, dual-beam oscilloscope with simultaneous audiomonitor. Photographic recordings were made with Grass kymograph camera. The sense organ was stimulated with a needle (45–50 μm tip diameter) mounted on a micromanipulator. The stimulus signal was monitored with a liquid junction potentiometer. Responses were simultaneously recorded from the pre-ganglionic and post-ganglionic sites. The right and left 6–7 connectives were completely isolated from the rest of the central nervous system by cutting the ventral nerve cord just caudad to the 6th ganglion.

RESULTS

The 7th abdominal ganglion is the last receiving station at the posterior end of the central nervous system (Babu, 1965). The sensory input from the telson, 5th and 4th metasomatic segments enters into this ganglion. The hairs, 3 and 4, of 5th metasomatic segment (see fig. 11 of Sanjeeva-Reddy, 1969) were stimulated. From Plate 1 A it is evident that the sensory axons do not terminate in the neuropile of the 7th ganglion but ascend up through the ipsilateral 6–7 connective. This is indicated by the fact that the time course of the response from both the sites is identical and that there is 1:1 correspondence between the units responding from both the sites. Conduction of this input through the 7th ganglion was found to be characterized by the lack of synaptic properties such as delay, lability, high threshold requirement, susceptibility to oxygen-lack and blocking by pharmacological agents such as nicotine and eserine. The responses recorded in Plate 1 B, from the sensory nerve (lower trace) and the contralateral 6–7 connective (upper trace), indicate that the primary sensory neurone, gives rise to collaterals in the neuropile of 7th ganglion which synaptically activate an interneurone ascending through the contralateral connective. The discharge of the contralateral interneurone (Plate 1 B) is highly phasic and occurs only during the discharge of the large, phasic sensory unit. This transmission from the ipsilateral primary sensory neurone to the contralateral interneurone was found to be very labile and exhibited all synaptic properties. Nicotine blocked the contralateral central response without affecting the ipsilateral sensory response. C and D in Plate 1 illustrate the stimulus-response relations of the ipsilateral 6–7 connective and the contralateral interneurone respectively. The ipsilateral sensory discharge consists of a large phasic unit restricted to the dynamic phase of the stimulus and a small tonic unit. By contrast, the contralateral central unit discharged only four impulses during the dynamic phase of the stimulus (Plate 1 D). From the stimulus waveform in D (Plate 1) it is evident that the hair was displaced at a relatively slow rate during the first stimulus compared with the second stimulus. The corresponding values for the mean interval of the impulse trains during the two stimuli are 10 and 7 msec respectively. Earlier studies (Sanjeeva-Reddy, 1969) have revealed the dependence of discharge frequency of the large sensory unit upon displacement velocity. Thus the velocity-sensitive nature of the discharge of the contralateral central unit indicates that this unit is the contra-

lateral, central representative of the large sensory unit. In view of the phase relations between the sensory and contralateral responses (Plate 1 B) also it may be inferred that the large sensory unit has driven the contralateral interneurone. The synapse mediating this excitation of a contralateral interneurone by the collaterals of a sensory neurone exhibits many-to-one ratio and hence can be considered as an integrating type.

DISCUSSION

The fact that the sensory neurones pass through the 7th ganglion of the scorpion is not surprising since primary sensory neurones are very commonly met with in the central connectives of insects (Fielden & Hughes, 1962; Mill, 1963) and crustaceans (Wiersma and his associates, 1955, 1958, 1960, 1961, 1963). But the demonstration of the origin of collaterals from the *en passant* sensory neurone is significant since such a situation has not been electrophysiologically demonstrated for the hair afferents of the insects and crustaceans. In several of the 'neurone schemes' proposed (Pumphrey & Rawdon-Smith, 1937; Roeder, 1948; Mill, 1963) some sensory neurones are represented as ipsilateral and others as contralateral in their central terminations. The possibility of a single sensory neurone giving rise to collaterals which synaptically activate a contralateral interneurone while passing through a ganglion has not been tested in insects and crustaceans. For the first time it has been shown in the scorpion that the collaterals from a single sensory neurone can activate a contralateral interneurone. Thus this work emphasizes the importance of parallel interactions in addition to the well-known serial interactions between neurones.

Another significant finding is that the input from a single hair is adequate to trigger the discharge of the interneurones of the scorpion whereas in crustaceans and insects several hairs should be stimulated to activate the interneurones. In this respect the scorpion is more suitable than the insect or crustacean for studies of the type reported here because a single sensory neurone associated with a single peripheral end organ can be clearly identified and its central effects studied. This basic difference in the organization of the tactile system of different arthropod groups illustrates that significant adaptive variations can exist between closely allied groups thereby giving fresh impetus to the comparative approach in understanding the functional organization of the arthropod nervous system.

In his anatomical work, Babu (1965) had shown that some sensory tracts from the segmental nerves of the 1st and 2nd abdominal ganglia move forward and ascend up to the preceding ganglion through the ipsilateral connective. No such ascending sensory neurones were reported by him in the neuropile of the 7th ganglion. Histological evidence is available for the presence of a sensory neurone which is contralateral in its terminations ('1' fibre of Babu & Venkatachari, 1966, and fibre 12 of Hanström, 1923). But no histological studies have so far shown the presence of a sensory axon which gives rise to collaterals while passing through a ganglion. Hence the results of the present investigation demonstrate the utility of the electrophysiological studies in supplementing as well as corroborating the cyto-architectural details assessed by the limited histological studies on the scorpion nervous system.

SUMMARY

1. As in the crustaceans and insects, so in the scorpion the primary afferent fibres constitute a considerable proportion of the axons in the central connectives.

2. The possibility of a sensory neurone sending collaterals, while passing through a ganglion, which activate a contralateral interneurone has been conclusively demonstrated. This type of activation differs from the pattern of contralateral activation so far demonstrated in the insects and crustaceans. In the latter groups, the available evidence indicates the activation of contralateral interneurones by the terminal branches of the sensory axons, but not by the collaterals.

3. It has been emphasized that in the scorpion, but not in insects and crustaceans, the tactile input from a single hair is adequate to trigger the central responses, which in itself is an advantage in analysing the integrative processes and functional connexions between neurones.

The electronic equipment used during the course of this investigation was obtained by Professor K. Pampapathi Rao through a joint research programme under an USAFOSR scheme. We wish to thank Professor T. H. Bullock for his help in procuring these instruments and Dr K. S. Swami, Head of the Zoology Department, Sri Venkateswara University, for providing the facilities.

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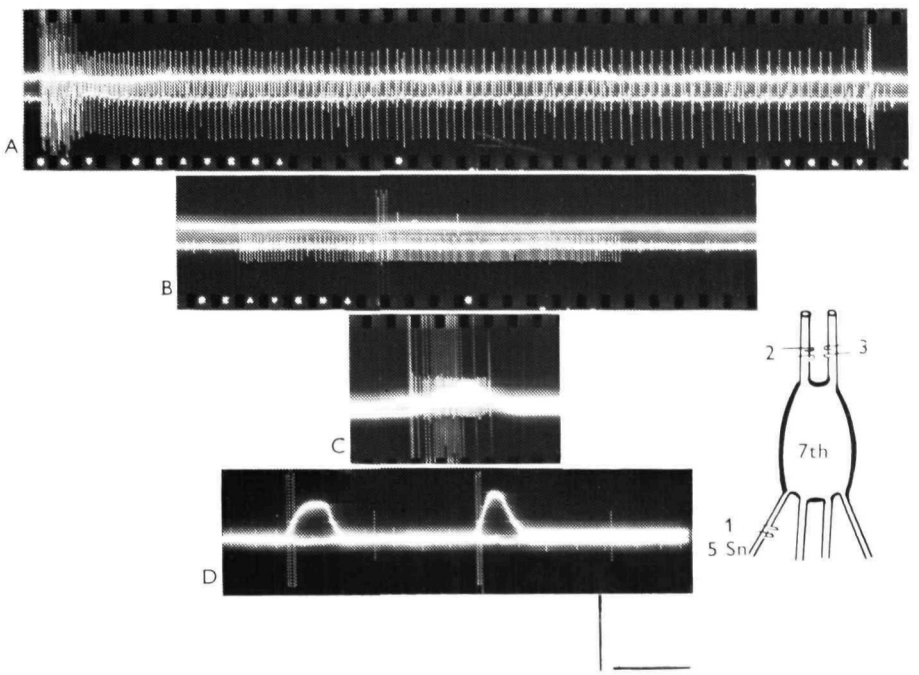
A
B
C
D
2
3
7th
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EXPLANATION OF PLATE

All records read from left to right and were made from the same preparation. Inset shows the 7th ganglion along with the 7–6 connectives and the most posterior of the segmental nerves which take their origin from it. Note the positions of recording electrodes. 7th = 7th abdominal ganglion; 5 Sn = 5th segmental nerve.

(A) 3rd hair on the ventro-lateral aspect of 5th metasomatic segment was displaced in cephalic direction. Upper beam shows the response from the ipsilateral (left) 6–7 connective isolated from the 6th ganglion (Recording site 2). Lower beam displays the response from the left 5th segmental nerve (Recording site 1). Calibration. Time = 150 msecs. Voltage = 88 μV, upper beam; 100 μV, lower beam.

(B) Same hair as in A displaced in cephalic direction. Upper channel shows the response of contralateral (right) 6–7 connective severed from 6th ganglion (Recording site 3). The response from the left 5th segmental nerve is displayed on the lower beam (Recording site 1). The smaller unit on the upper beam is spontaneous in origin. Calibration. Time = 300 msecs. Voltage = 214 μV, upper beam; 150 μV, lower beam.

(C) The hair on the opposite side of 5th metasomatic segment, i.e. 4th hair, symmetrical to the one stimulated in A and B was displaced in cephalic direction. The response from the ipsilateral (right) 6–7 connective (Recording site 3) is displayed on the upper beam. Lower signal represents the stimulus waveform. Calibration. Time = 300 msecs. Voltage = 100 μV, upper beam.

(D) Same hair as in A and B displaced in cephalic direction. Response of the contralateral (right) 6–7 connective (Recording site 3) is displayed on the lower beam. Notice that about three units are spontaneously discharging. The upper signal indicates the stimulus waveform. Calibration. Time = 300 msecs. Voltage = 100 μV, lower beam.