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SHORT COMMUNICATION

A LOCAL INTERNEURONE WHICH RECEIVES DIFFERENTIAL INPUT FROM THE MEDIAL AND LATERAL GIANT AXONS

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The crayfish ventral nerve cord contains two pairs of giant axons which are termed command axons for escape because impulses in either pair of cells trigger a complex series of neural events that culminates in a rapid flexion and extension of the abdomen, i.e. a 'tailflip' (Wine & Krasne, 1982). Each pair of axons triggers a specific trajectory of escape by virtue of differences in its intersegmental pattern of synapses with flexor motor neurones (Larimer, Eggleston, Masukawa & Kennedy, 1971; Wine & Krasne, 1972; Mittenthal & Wine, 1973; Miller, Hagiwara & Wine, 1985; Dumont & Wine, 1987*b*). However, while some of the flexor motor pathways are differentiated in a way that is consistent with the observed behaviour, a persistent puzzle has been the extraordinary degree of overlap in the output connections of the two kinds of giant axons to other portions of the flexor motor pathway. These overlapping connections should blur the distinction between the escape trajectories, and thus are inconsistent with the observed behaviour.

The inconsistencies between neural connectivity and behaviour have slowly been resolved: it has been shown in several instances that the inconsistent connections are not expressed behaviourally either because they are too weak or because they are inhibited (Kramer, Krasne & Wine, 1981; Dumont & Wine, 1987*b*). However, this resolution has raised its own set of problems, including why the inconsistent connections persist, how inhibition of the inappropriate connections evolved, and whether inhibition can be turned off under some circumstances so as to switch the output pattern of the command cells. One difficulty in answering these questions has been the difficulty in identifying *any* central neurones that are differentially recruited by the giant axons. Table 1A lists the identified neurones that are known to be excited following stimulation of either giant axon. Table 1B shows that, until now, only a small number of efferents and no central neurones were known to be differentially excited by the lateral giant and medial giant axons.

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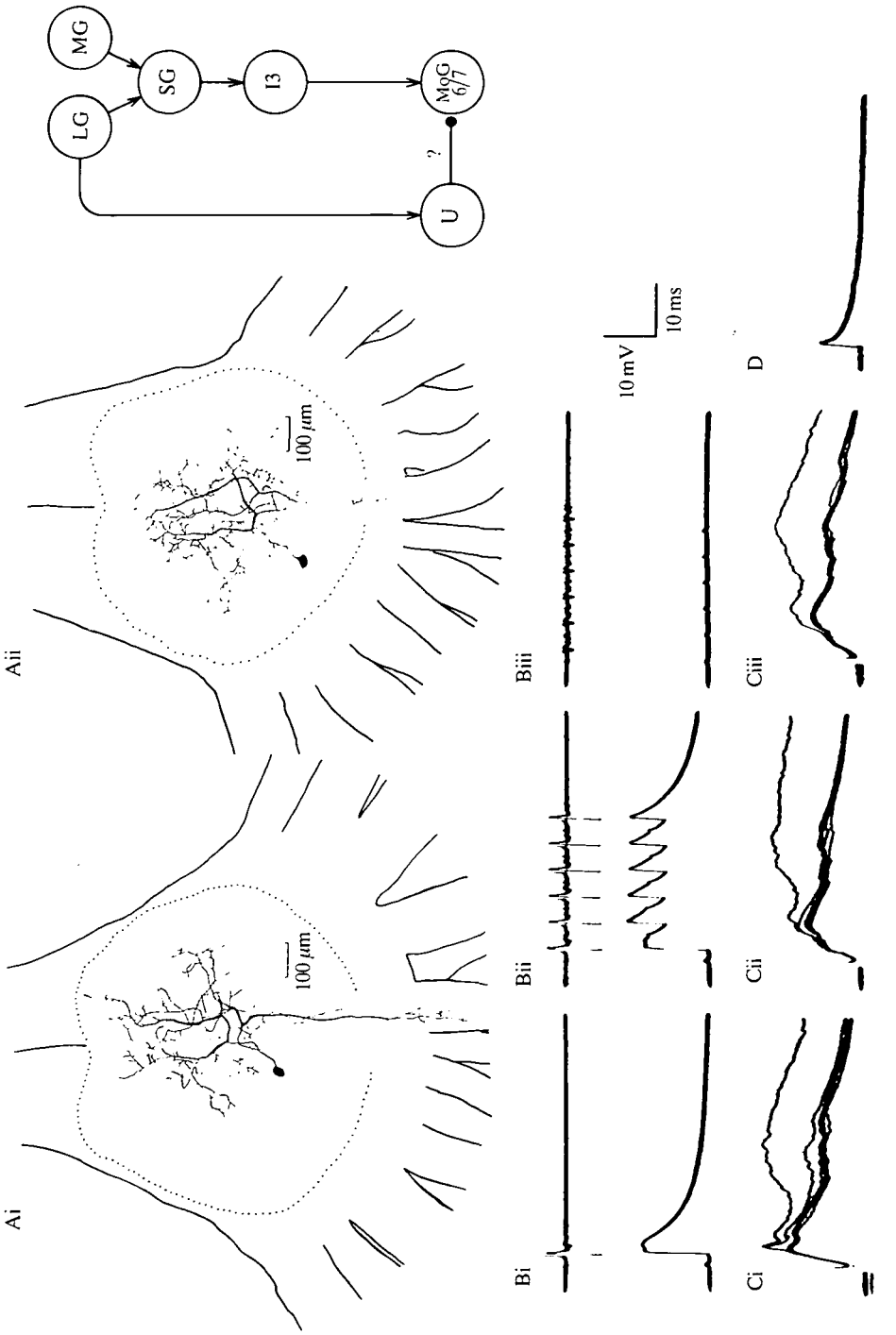
MG
LG
SG
I3
MoG 6/7
?
U
Ai
Aii
100 μm
100 μm
Bi
Bii
Biii
Ci
Cii
Ciii
D
10 mV
10 ms

Fig. 1

Table 1A. *Central neurones affected in common by LGs and MGs*

Central neurones excited	
Segmental giants	Roberts *et al.* 1982
Corollary discharge interneurones	Kramer, Krasne & Wine, 1981
Motor giant inhibitors	Wine, 1977
C-cell	Kirk, Dumont & Wine, 1986
Primary afferent depolarizing interneurones	Kirk & Wine, 1984
Central neurones inhibited	
Interneurone A	Krasne & Bryan, 1973
MGs	Roberts, 1968
LGs	Roberts, 1968

Table 1B. *Central neurones affected differentially by LGs and MGs*

Central neurones excited	
U-cell	Takahata & Wine (this paper)
Central neurones inhibited	
None known	

We have now identified a local interneurone that is fired by the lateral giants but not the medial giants. The interneurone is provisionally termed a 'U-cell' because of its characteristic U-shaped dendrite. Fig. 1Ai,ii shows the structure of the U-cell in the sixth abdominal ganglion in which a suprathreshold EPSP and superimposed spike were recorded following a directly elicited spike in the lateral giant axons (Fig. 1Bi). The response had a latency of 0·4 ms measured from the lateral giant spike recorded at the anterior margin of the terminal ganglion, and was quite stable, following without decrement at frequencies of 200 Hz (Fig. 1Bii).

The U-cell did not respond to impulses in the medial giant axons (Fig. 1Biii). It was evident that the medial giant axons were actually stimulated and were conducting into the sixth ganglion because an extracellular electrode placed on the nerve cord just anterior to the ganglion recorded their spikes (Fig. 1Biii, top trace), and a single medial giant spike elicited an action potential in a sixth ganglion motor neurone (not shown).

Fig. 1. A local interneurone that is excited by the lateral giants but not by the medial giants. (Ai,ii) Structure of the cell from different animals. The cell was filled with Lucifer Yellow after electrophysiological recordings. Drawings show horizontal views. Inset indicates hypothetical role of the cell as a feedforward inhibitor of the telson motor giants. LG, lateral giant; MG, medial giant; SG, segmental giant; I3, identified corollary discharge interneurone; MoG, motor giants. (Bi,ii) The response of the cell to directly elicited lateral giant spikes. (Biii) Lack of responses to medial giant spikes, which were identified by recording them directly in the connectives under visual control, and by their ability to fire a putative telson motor giant neurone. (Ci–iii) Responses to stimulation of contralateral nerve 5, nerve 4 and nerve 2, respectively. Stimulation was repeated at 1 Hz; five superimposed traces are shown for each test. (D) Antidromic spike elicited by direct stimulation of the axon terminal in nerve 6. Records shown in B and C were obtained from the Ai cell and record in D was from the Aii cell.

We have encountered this type of cell only twice, but the physiological and structural data were virtually identical in the two cases. The differential response uniquely identifies the U-cell in our experience, but the number of cells with similar properties is unknown. The rarity with which the cell has been encountered may argue for a relatively small number. The site of electrode impalement was on the midline, in one of the constricted portions of the neuropilar branches. On the basis of the very large amplitude of the EPSPs and the very small spikes, we interpret the penetration site to be a dendrite located several length constants from the spike initiation site (Reichert *et al.* 1982).

Several other aspects of this cell's physiology are pertinent to a hypothesis about its function. It was spontaneously active at a frequency of approximately 10 Hz and was fired by electrical stimulation of sensory nerves from the tailfan (Fig. 1Ci–iii). The extent of its receptive field was not determined beyond showing that both sides of the telson (i.e. areas innervated by nerves 4 and 5) as well as the region of the uropods innervated by nerve 2 are excitatory.

We do not know the function(s) of this cell. However, all of its anatomical and physiological features are consistent with the hypothesis that it is an inhibitor of the telson motor giants. The most striking aspect of the cell's anatomy is its axon, which terminates in the proximal portion of nerve 6, a purely motor nerve innervating the telson muscles. The cell could be antidromically excited by directly stimulating this terminating axon (Fig. 1D). This anatomical pattern suggests that the axon is synapsing on the distal portion of one or more telson flexor motor neurone axons, close to their presumed sites of impulse initiation. A very similar pattern of axon branching has been noted for the intersegmental motor giant inhibitor (Wine, 1977 and unpublished results) and for the C-cell (Kirk, Dumont & Wine, 1986), both of which are inhibitors of the motor giant. Indeed, command-derived postsynaptic inhibition has not been demonstrated for any other fast flexor motor neurone. There is additional physiological data that fits with the cell's anatomy and physiology. The existence of a local, spontaneously active cell that is presynaptic to the motor giants was established by simultaneous recordings in the motor giants of adjacent ganglia (Sherwood & Wine, 1979; Dumont & Wine, 1987*a*), and it is also known that the motor giants receive synaptic input, presumed to be inhibitory, following sensory stimulation (Sherwood & Wine, 1979).

Although the function of the U-cell must remain hypothetical, it is clear that it is fired by the lateral giants and not the medial giants. Since the telson motor giants are fired by the medial giants and not by the lateral giants, our hypothesis that this cell inhibits the motor giants would be consistent with the behavioural patterns produced by each giant axon.

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