

deprived of drinking water for 72 h (water-deprived). In the experiments rabbits were exposed for 1 h to a  $T_a$  of 35°C.  $T_{re}$  and oxygen consumption ( $V_{O_2}$ ) were monitored continuously. Respiratory volumes and frequencies were measured at 10-min-intervals using the barometric technique of Drorbaugh and Fenn<sup>6</sup>.

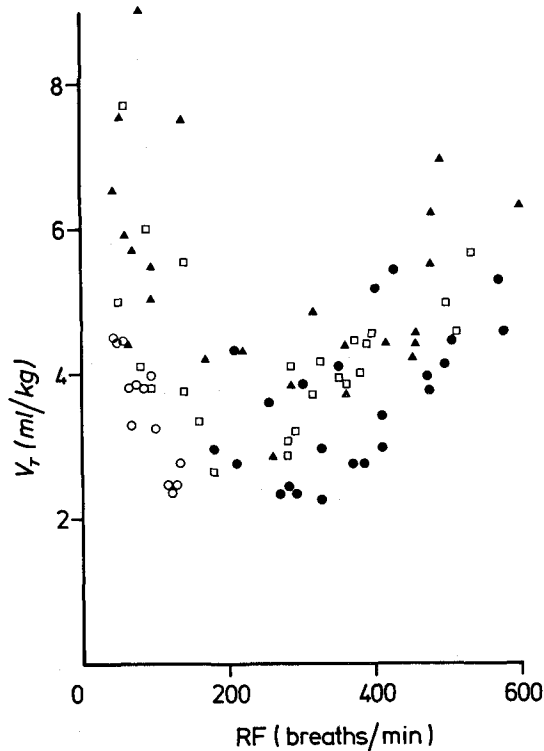


Fig. 3. The relationship between respiratory frequency (RF) and tidal volume ( $V_T$ ) in rabbits exposed to 35°C (symbols as in figure 1) and to temperatures within the thermoneutral range (○).

Figure 1 demonstrates the correlation between  $T_{re}$  and  $V_E$ . Differences between the 3 conditions are not significant, thus it appears that  $V_E$  is always regulated at a level appropriate to a given core temperature. RF increases with increasing  $T_{re}$  (figure 2a).  $V_T$  initially decreases with increasing  $T_{re}$  then increases with a further rise in  $T_{re}$  (figure 2b). The minimum  $V_T$  for control, cold-exposed and water-deprived rabbits occurs at rectal temperatures of 39.3, 39.8 and 40.2°C respectively. At these rectal temperatures, the corresponding respiratory frequencies average 300, 250 and 265 breaths/min. Plotting RF against  $V_T$  (figure 3) confirms that  $V_T$  is lowest in the RF range 250–300 breaths/min. Above this range, thermoregulatory demands dictate that both RF and  $V_T$  increase in order that  $V_E$  be maintained at the appropriate level. Below RF = 250 it might be argued that  $V_T$  is physically dependent upon RF such that a low RF will inevitably lead to a high  $V_T$ . To test this possibility, the same rabbits were exposed to ambient temperatures within their thermoneutral range ( $T_a$  21–27°C). In these experiments RF varied over a range of between 45 and 135 breaths/min but although the trend is still for  $V_T$  to be higher for a lower RF, mean  $V_T$  remains significantly lower than in blocked rabbits at the corresponding frequencies when exposed to 35°C ( $p < 0.001$ ) (see figure 3). Moreover, this difference could not be explained in terms of a change in metabolic requirements as the difference in  $V_{O_2}$  between the animals at 35°C and at thermoneutrality was not great enough to account for the difference in  $V_T$ . Thus the conclusion is reached that in the rabbit the thermoregulatory drive is so powerful that when an increase in RF in the heat is specifically inhibited by water deprivation of prior cold exposure, then  $V_E$ , and presumably  $E_{ex}$ , can be increased through a rise in  $V_T$ .

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## Electrotonic synapses in the visceral ganglion of *Planorbis*<sup>1</sup>

V. W. Pentreath<sup>2</sup> and M. S. Berry

Wellcome Laboratories of Pharmacology, Gatty Marine Laboratory, The University of St. Andrews, St. Andrews (Scotland), 24 August 1976

**Summary.** In the visceral ganglion of *Planorbis* the postsynaptic neurones of the characterized dopamine neurone are connected by non-rectifying electrotonic junctions. The coupling, which is reduced by stimulation of the dopamine neurone and by applied dopamine, may be important in the generation of burst activity. Specialized areas of close apposition of membranes in the neuropile are considered to be the morphological correlate of electrotonic coupling.

In the left pedal ganglion of the water snail *Planorbis* corneus there is a specified dopamine neurone which makes monosynaptic connexions with certain neurones in the visceral and parietal ganglia<sup>3,4</sup>. The input from the dopamine neurone is inhibitory to the visceral neurones and excitatory to the parietal neurones. The visceral neurones (of which there are at least 15) have been found to be coupled electrically. This paper describes some aspects of the coupling and also its presumed morphological correlate. **Materials and methods.** The isolated ganglionic ring was immersed in physiological saline<sup>5</sup> at room temperature (20°C). Double barrelled microelectrodes containing 0.6 M  $K_2SO_4$  were used for intracellular recording and

stimulation. The recording and stimulating equipment was conventional. For electron microscopy the visceral ganglion was fixed in buffered glutaraldehyde and osmium solutions<sup>6</sup>. Sections were stained with lead citrate

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- 2 Present address: Department of Biology, University of Salford, Salford, M5 4WT.
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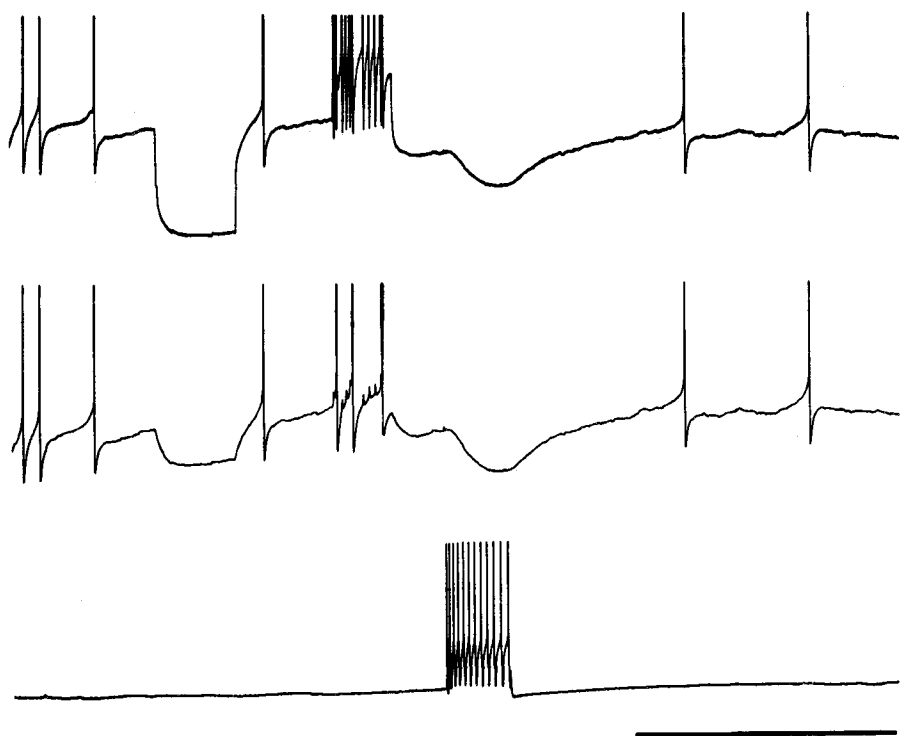


Fig. 1. Simultaneous intracellular recordings from the dopamine neurone (lower trace) and 2 postsynaptic neurones (upper and middle traces). Stimulation of the dopamine neurone produces smoothly summing ipsps in both postsynaptic neurones. Hyperpolarizing and depolarizing pulses applied to 1 postsynaptic neurone (upper) are transmitted to the other (middle). Spikes produce small depolarizing potentials. During spontaneous activity the action potentials in the 2 neurones were in synchrony. Note that the spikes elicited by the depolarizing pulse in the upper trace form 3 bursts whose termination coincides with spikes in the middle trace. With lower depolarizing current the interburst interval was longer but each burst always terminated whenever the neighbouring neurone fired. Time scale, 10 sec; voltage scales, 25 mV.

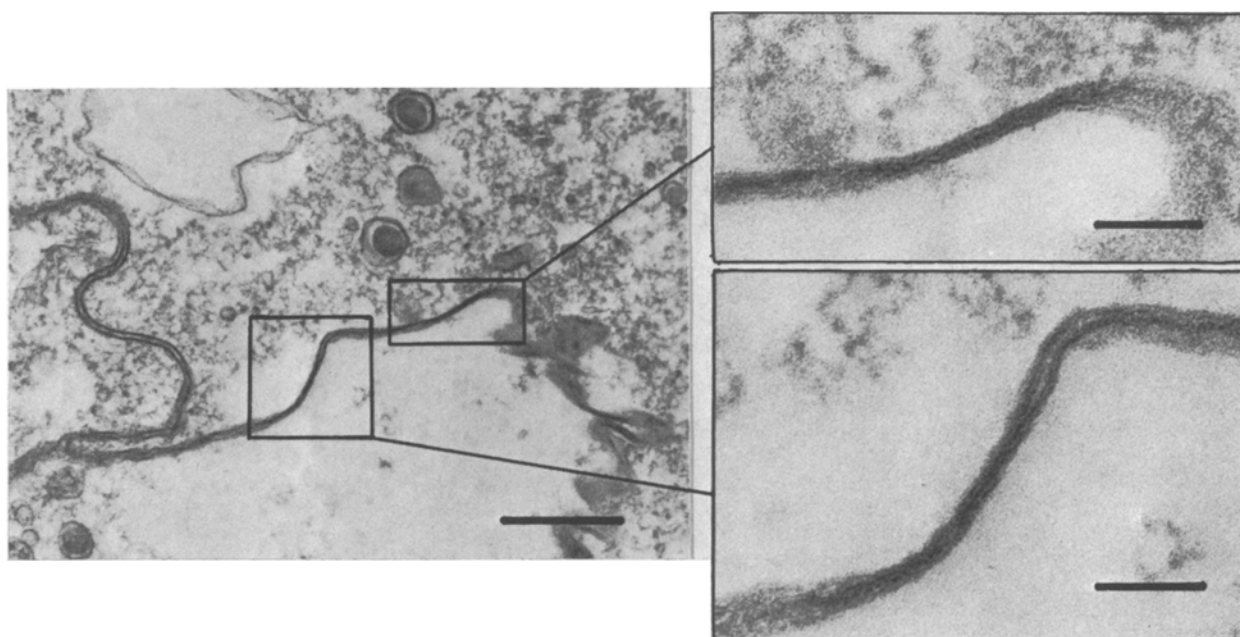


Fig. 2. Electron micrographs of part of the neuropile in the visceral ganglion of *Planorbis corneus*. The membranes of 2 adjacent processes come into close contact in the areas indicated by the insets, which are shown at high magnification on the right. The cytoplasm of the apposed processes is relatively empty, although dense-cored vesicles are present in the upper process. The scales represent 0.5  $\mu\text{m}$  (left micrograph) and 0.1  $\mu\text{m}$  (right micrographs).

and uranyl acetate and examined in a Phillips 301 electron microscope.

**Results and discussion.** The coupling between postsynaptic neurones of the dopamine neurone is illustrated in figure 1. Hyperpolarizing and depolarizing current pulses in any one neurone are transmitted to the others. Spikes produce small transmitted potentials (epsps) which may reach threshold individually or more usually by summation. Coupling coefficients for different pairs of neurones were very variable, ranging from nearly 0 up to 0.5 (coupling coefficient is the post-/presynaptic potential<sup>7</sup>). The strength of coupling does not depend on the proximity of the somata. There is little change in the electrotonic epsps when the ganglia are bathed in saline containing no Ca, 6 times normal Mg and 1 mM EGTA; this indicates the absence of any chemical component.

During ipsps produced by stimulating the dopamine neurone the strength of coupling between postsynaptic neurones is considerably reduced. The addition of dopamine ( $10^{-5}$  M) to the bath produces the same effect. This is similar to the synaptic decoupling first described in Navanax by Spira and Bennett<sup>8</sup>; the decoupling is thought to be important in enabling the neurones to fire independently of each other<sup>8-10</sup>. It is not known whether decoupling has a similar function in Planorbis.

The postsynaptic neurones often fire spontaneously in couplets of spikes. Maintained depolarization of one of the neurones usually results in longer bursts. Burst formation is a property of a number of electrically coupled groups of neurones and may result from the intrinsic properties of non-rectifying electrotonic synapses rather than endogenous bursting activity of individual neurones<sup>11-14</sup>. For example, Getting and Willows<sup>11,12</sup> have shown that bursts in electrically coupled neurones in Tritonia develop by regenerative excitation within the network and are terminated when a majority of neurones fire in near synchrony; synchronization results in a net hyperpolarization caused by an accentuation and prolongation of the spike after-hyperpolarization due to a

reduction in junctional shunting. In Planorbis burst termination is almost always accompanied by the synchronous firing of another recorded neurone in the network (figure 1) suggesting that a similar mechanism is operating.

Electron microscopic examination of the visceral ganglion revealed occasional areas of close apposition of neuronal membranes in the neuropile (figure 2). At high magnification the outer stained layer of each apposing membrane appeared to touch. By analogy with data in other systems<sup>15,16</sup> these points of membrane apposition were considered to be morphological counterparts of electrotonic coupling. They were not observed between neurone somata or in nerve tracts, but it was not possible to determine whether they were axodendritic, axoaxonic or dendrodendritic.

The results indicate that electrotonic coupling between postsynaptic neurones of the dopamine neurone occurs at specialized areas of apposition in the neuropile. The coupling synchronizes the firing of a proportion of the neurones, and may be important for the generation of burst activity.

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## Electrophysiological evidence for chemosensitivity to adenosine, adenine and sugars in *Spodoptera exempta* and related species

W. C. Ma<sup>1,2</sup>

*ARC Unit of Insect Physiology, Department of Zoology, University of Oxford, Oxford OX1 3PS (England), 31 August 1976*

**Summary.** Electrophysiological studies show that *Spodoptera exempta* and closely related species possess a receptor with specific sensitivity towards adenosine and adenine. 2 other types of receptors responded to certain sugars. The functional significance of these receptors in controlling chemoresponses of the larvae is discussed.

Adenosine and sucrose, isolated from maize plants, have recently been identified as strong phagostimulants for the African armyworm, *Spodoptera exempta*<sup>3</sup>. This harmful Noctuid feeds exclusively on grasses (Gramineae, Cyperaceae)<sup>4</sup>. Other studies on this species indicated that the maxillary styloconic sensilla play an important part in the food discriminative behaviour<sup>5,6</sup>. Evidence for the function of the styloconic sensilla in determining the chemosensitivity of *S. exempta* to adenosine and sugars is presented in this paper.

**Materials and methods.** Diet-reared 1-2 days old last-instar larvae were used throughout. For electrophysiological recording the tip-recording technique<sup>7</sup> was employed with conventional methods of amplification and

registration of signals. A receptor 'response' is defined here as the number of impulses generated in 1 sec beginning 50 msec after the onset of stimulation.

**Results and discussion.** Adenosine evoked slowly adapting trains of action potentials from a receptor located in the lateral sensilla of *S. exempta* (figures 1 and 2). Sodium chloride, which had been added to the stimulus solution at 0.1 M in order to improve the conductance properties in the stimulating-recording pipette, elicited an essentially different response pattern in these sensilla (figures 1 and 4). The concentration-response relation of the adenosine-sensitive receptor (figure 3) indicated a sensitivity threshold between  $10^{-4}$  and  $10^{-5}$  M, while saturation was reached at about  $10^{-2}$  M adenosine (figures 2 and 3). The