within the blastocyst tissue of aromatase, 17–20 desmolase and 3-sulphatase enzyme systems concerned with the production of oestrogens from neutral steroids, progesterone and conjugated steroids, respectively. Evidence has also been obtained for the presence of other enzyme systems involved in the formation of steroid conjugates other than the sulphates of oestrone and oestradiol-17β. These findings indicate that the presence of unconjugated oestrogen and progesterone in blastocyst tissue is probably a result of their synthesis *in situ* and not a result of their diffusion from the maternal circulation. Thus, even at this early stage of development, the pig blastocyst has the enzymatic capacity to produce biologically important steroid hormones. It remains to be seen whether the local effect of hormones produced by the blastocyst is, in some way, concerned with the ongoing process of implantation or with the signal whereby the developing embryo conveys its presence to the mother. This latter event may be related to an alteration in the pattern of uterine metabolism.

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1 Huff, R. L., and Eik-Nes, K. B., *J. Reprod. Fert.*, **11**, 57 (1966).
2 Lutwak-Mann, C., in *The Biology of the Blastocyst* (edit. by Blandau, R. J.), 252 (The University of Chicago Press, 1971).
3 Seamark, R. F., and Lutwak-Mann, C., *J. Reprod. Fert.*, **29**, 147 (1972).
4 Perry, J. S., and Rowlands, I. W., *J. Reprod. Fert.*, **4**, 175 (1962).
5 Dhindsa, D. S., and Dziuk, P. J., *J. Anim. Sci.*, **27**, 122 (1968).
6 Crombie, P. R., thesis, University of Cambridge, 1972.
7 Challis, J. R. G., Heap, R. B., and Illingworth, D. V., *J. Endocr.*, **51**, 333 (1971).
8 Heap, R. B., Gwyn, M., Laing, J. A., and Walters, D. E., *J. agric. Sci., Camb.*, **81**, 151.
9 Abraham, G. E., Swerdloff, R., Tulchinsky, D., and Odell, W. D., *J. clin. Endocr. Metab.*, **32**, 619 (1971).
10 Challis, J. R. G., Harrison, F. A., and Heap, R. B., *J. Endocr.*, **57**, 97 (1973).
11 Brinster, R. L., *J. Reprod. Fert.*, **10**, 227 (1965).
12 Bedford, C. A., Harrison, F. A., and Heap, R. B., *J. Endocr.*, **55**, 105 (1973).
13 Challis, J. R. G., Harrison, F. A., and Heap, R. B., *J. Endocr.* (in the press).

Electrical Coupling across Developmental Boundaries in Insect Epidermis

The polarity of the surface folds on the abdominal cuticle of the insect *Rhodnius*, which normally run at right angles to the antero-posterior axis, is controlled by the underlying epidermal cells. When portions of integument are transplanted or rotated the epidermal cells produce surface folds the orientation of which shows that the cells "remember", at least to some extent, their original polarity[1,2]. Such experiments also suggest that the cells have access to information which defines the spatial pattern of differentiation within each segment[3]. It has been suggested that a gradient of some property exists which is reiterated from segment to segment so that the intersegmental border intervenes between the "high" part of one gradient and the "low" of the next. In one model the segmental gradient is viewed as a concentration gradient of a diffusible morphogen[2-5]. Studies in a closely related insect have shown that from a very early stage the segments have independent lineages, clones stopping abruptly at the intersegmental border[5,6].

It has often been suggested that molecules conveying the information necessary for defining the spatial pattern of differentiation may pass from cell to cell via low electrical resistance pathways[7-9]. There is little evidence to support these ideas, although Dixon and Cronly-Dillon[10] have reported that gap junctions disappear from the central retina of *Xenopus* at the time of determination of retinal polarity. (The presence of gap junctions in cultured cells has been correlated with the ability to exchange small molecules such as nucleotides, and with low resistance intercellular pathways[11].) Any morphogen controlling differentiation in the insect segment could pass from cell to cell via low resistance junctions, although the independent behaviour of each segment requires that the movement of the morphogen be restricted to cells within the same segment. We have therefore examined whether low resistance intercellular pathways exist within each segment and from one segment to the next.

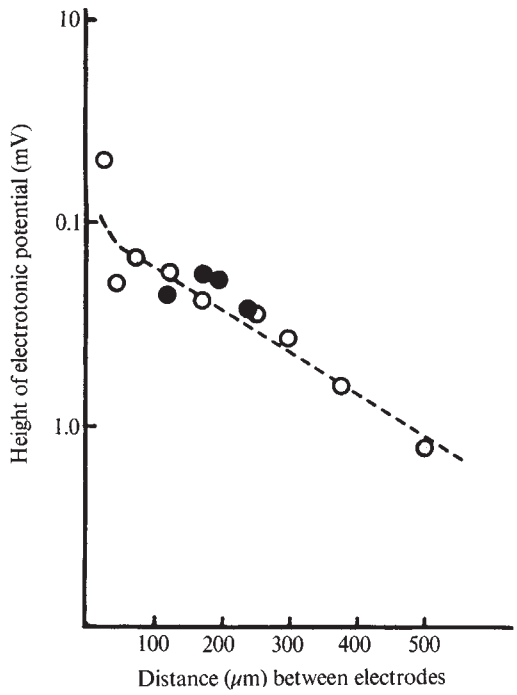

Fig. 1 Spread of ionic current in the insect epidermis. Ordinate: Height of the electrotonic potential (mV). Abscissa: Distance between current passing and voltage recording electrodes (μm). ○, Measurements with both electrodes in the same segment; ●, electrodes in adjacent segments. Line drawn through the points calculated according to

$$V = \frac{IR_i}{4d} j\, H_0^{(1)}(j\, r/\lambda)$$

where V is the height of the electrotonic potential, I the injected current, d the thickness of the sheet, r the interelectrode distance and λ the space constant of the preparation (given by $\sqrt{R_m/R_i d}$ where R_m and R_i are the specific resistances of the surface membrane and intercellular pathway respectively). λ set at 350 μm; $H_0^{(1)}$ is a tabulated Bessel function[13].

Third stage larvae of *Rhodnius* were used 3–5 d after feeding. The dorsal integument of the abdomen was removed (approximately 5 × 3 mm), and the fat body and basement membrane stripped off. Examination in the electron microscope showed a monolayer of epidermal cells (about 10 μm in diameter) continuous across the intersegmental border. This preparation was pinned out flat in Jones and Cunningham medium[12] epidermal cells uppermost and viewed in a Zeiss dissecting microscope (×100). Glass microelectrodes filled with 3 M KCl or 0.8 M K citrate (tip potential < -8 mV; resistances 40-60 MΩ) were used. Current pulses were injected into one cell and the voltage deflexion produced in a nearby cell recorded by a second intracellular microelectrode. Membrane potentials were routinely recorded on insertion of each electrode and one electrode was then switched over to current injection to ensure that both current passing and voltage recording electrodes lay inside a cell.

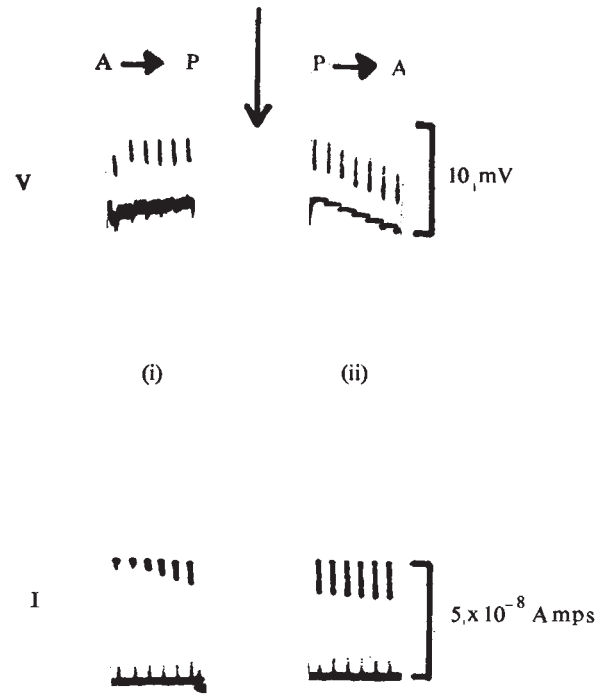

Fig. 2 Electrical coupling across the intersegmental border. In each case the upper record gives the resting membrane potential (lower margin) and the final height of the electrotonic potential (upper margin) at the end of a one second current pulse recorded on a slowly moving pen recorder. The lower record gives the magnitude of the injected current pulse. Depolarizing current pulses were passed. (i) Electrotonic potential recorded with current passing electrode in anterior part of one segment and voltage recording electrode across intersegmental border. (ii) Current passing switched onto the voltage recording electrode and *vice versa*, so current now injected in posterior part of one segment and recorded in anterior part of the next. Distance between electrodes = 125 μm.

Intracellular membrane potentials ranged from −6 to −30 mV with a mean of −17 mV (±5.0 mV s.e.m.; n=61). Input resistances (measured with an electrode separation of <25 μm) were in the region of 10^6 Ω; on no occasion were the current passing and voltage recording electrodes in the same cell. After determination of the input resistance of the preparation the inter-electrode distance was increased gradually and the height of the electrotonic potential measured.

Preparations were tested for the spread of ionic current both within the same segment and across the intersegmental border. In all preparations (n=13) electrical coupling has been observed both between cells in the same segment and between cells in adjacent segments. A semi-logarithmic plot of the height of the electrotonic potential against the inter-electrode distance for one of these preparations is shown in Fig. 1. For this series of measurements the current passing electrode was placed in a cell in the posterior part of one segment and current spread measured away from this electrode in both anterior and posterior directions. The measurements made within the same segment and those made with the intersegmental border interposed between the electrodes fall along the same line, suggesting that the border does not present a significant barrier to the movement of ions from one segment to the next. The line drawn through the points in Fig. 1 was calculated using a solution of the cable equations for current spread from a point polarizing electrode into a flat sheet[14] taking a space constant of 350 μm. When injection of current was switched from one electrode to the other so that current passed first in the anterio-posterior direction and then in the reverse direction across the barrier (Fig. 2) the size of the electrotonic potential did not change; there was no evidence for rectification.

The cells of the insect epidermis secrete a waxy epicuticle which is highly impermeable to both water and ions[15,16]. The possibility that a shunt for the flow of ionic current exists in the extracellular space between the cells and this high resistance cuticle must not be overlooked. If such a shunt existed it could give rise to apparent electrical coupling between the cells because of ion current flow from one cell to the next via a restricted extracellular pathway.

Wigglesworth[16] has shown that superficial abrasion renders the cuticle permeable to water. We have found that normal membrane potentials and electrical coupling within and between segments persist after heavy surface abrasion, which allows neutral red to penetrate the cuticle and enter the cells, showing that they are not damaged by this treatment. The input resistances of these epidermal cells were not markedly different from those in unabraded preparations. The intercellular coupling illustrated in Fig. 1 is thus the result of low resistance connexions between the cells and is not the consequence of a restricted extracellular pathway. There is, therefore, effective electrical coupling, both between cells situated in the same segment, and between cells in adjacent segments; suggesting that there is no simple correlation between the independent development of adjacent organs and the presence of an intervening barrier to the movement of small ions.

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1 Locke, M., *J. exp. Biol.*, **36**, 459 (1959).
2 Lawrence, P. A., Crick, F. H. C., and Munro, M., *J. Cell. Sci*, **11**, 815 (1972).
3 Lawrence, P. A., *Symp. Soc. exp. Biol.*, **25**, 379 (1971).
4 Lawrence, P. A., *J. exp. Biol.*, **44**, 607 (1966).
5 Lawrence, P. A., *Nature new Biol.*, **242**, 31 (1973).
6 Lawrence, P. A., *J. Embryol. exp. Morph.* (in the press).
7 Furshpan, E. J., and Potter, D. D., *Curr. Top. dev. Biol.*, **3**, 98 (1968)
8 Goodwin, B. C., and Cohen, M. H., *J. theor. Biol.*, **25**, 49 (1969).
9 Loewenstein, W. R., *27th Symp. Soc. dev. Biol.* (edit. by Locke, M.) (Academic Press, New York, 1969).
10 Dixon, J. S., and Cronly-Dillon, J. R., *J. Embryol. exp. Morph.*, **28**, 659 (1972).
11 Gilula, N. B., Reeves, O. R., and Steinbach, A., *Nature*, **235**, 262 (1972).
12 Jones, B. M., and Cunningham, I., *Exp. Cell Res.*, **23**, 386 (1961).
13 Jahnke, E., and Emde, F., *Tables of Functions with formulae and curves*, 3rd ed. (Tuebner, Leipzig, Berlin, 1938).
14 Noble, D., *Biophys. J.*, **2**, 381 (1962).
15 Wigglesworth, V. B., *Quart. Jl microsc. Sci.*, **76**, 270 (1933).
16 Wigglesworth, V. B., *J. exp. Biol.*, **21**, 97 (1945).

Optimal Fish Cruising Speed

THE life cycles of various species of fish include long range migrations for feeding and spawning purposes. Long stretches of these migratory routes are often crossed without food intake so that efficient use of the store of internal energy is essential to survival. Many such migratory species have produced various adaptations for efficient swimming such as streamlining and carangiform[1] body movements. Schooling, which is also common among long distance swimming species[2], has been shown to contribute to the locomotory performance[3]. Here I show that regulating the swimming speed can increase the performance and efficiency of motion by appreciable amounts.

Such theoretical predictions of optimal cruising speeds can be of aid in tracking and locating fish during migrations for fishing purposes and so on. Fishes have two propulsive mus-