beyond this level ACh causes a potential change in the reverse direction from the normal. The "reversal" potential for the action of a particular drug or transmitter depends on the changes in the ionic permeability of the membrane produced by the interaction of the drug with its receptors. These changes can be deduced from the effect of altered ionic media on the position of the null point; in the case of ACh acting at the end-plate, the permeability to sodium and potassium ions only is increased by the transmitter.

In their second article, Feltz and Mallart describe experiments in which they used similar techniques to determine whether the same permeability changes are produced by the action of ACh at the extra-junctional receptors of normal frog muscles and at those induced by denervation. The results showed that although responses at both these types of receptors are also mediated exclusively by changes in cationic permeability, they have a reversal potential which is substantially more negative (-40 to -50 mV) than that observed at the normal neuromuscular junction.

The most rational explanation for this is that, during junctional and non-junctional responses, the permeabilities to sodium and potassium are altered relative to each other in a different fashion, thus indicating a real difference in ionic selectivity between junctional and non-junctional receptors. This selectivity could be caused by an altered association outside the end-plate between receptors and ion channels which have been opened up during their activation ("ionophores"), or by a genuine difference in the receptors themselves. Pharmacological studies have indicated that the ACh receptors which are induced after denervation are less sensitive to curare (Beranek and Vyskocil, *J. Physiol.*, **188**, 53; 1967), and of interest also are the recent experiments of Miledi and Potter (*Nature*, **233**, 599; 1971) on the binding of α -bungarotoxin to muscles. These studies suggest that two different classes of ACh receptor may exist at the end-plate itself, one of which has a low affinity for curare, and might therefore be analogous to the "slow-rise-time", "more-negative-reversal-potential" receptors of Feltz and Mallart. The toxin also binds to receptors induced after denervation, and its use will, no doubt, make possible their isolation and characterization, as well as that of the junctional and extra-junctional receptors of normal muscle. In the meantime, however, the discovery of measurable differences in the responses of these classes of receptor must stimulate further study of the influences which determine their formation.

PLANT PHYSIOLOGY

Phloem Transport

from a Correspondent

It may seem surprising that after more than forty years of intensive study by some of the most able plant physiologists of the day, the mechanism whereby organic substances, notably sugars, are transported in the phloem of plants is still unknown. The reason why this problem is unsolved is not hard to find. Transport occurs through narrow pipes—the sieve tubes—which, unlike the xylem vessels through which water moves, are alive and very sensitive to disturbance which readily leads to loss of function. Moreover, normal transport occurs only when the sieve tubes are connected at their ends with living cells which supply and receive the transported materials and there are some indications that association with living cells along the conducting strand is also essential. With such a complex multi-cellular system it is very difficult to obtain experimental results which can be interpreted unequivocally. Phloem transport is therefore an ideal subject for lively discussion, as was shown at a meeting organized by the Physicochemical and Biophysical Panel of the Society of Chemical Industry held in London on October 18 under the chairmanship of Professor P. E. Weatherley.

The most widely supported mechanism is still the one advocated in 1930 by the German botanist, Münch, and now usually referred to as "pressure flow". According to this hypothesis, movement of sugar into a sieve tube at one end (the source) and its removal at the other (the "sink") causes, by osmosis, a difference in hydrostatic pressure between the two ends and leads to a mass flow of water and dissolved substances along the tube.

A major drawback to the pressure flow hypothesis, as was pointed out at the meeting by Dr D. C. Spanner (Bedford College, London), is that if there are obstacles in the sieve tube lumen which significantly increase its resistance to linear flow, the pressure gradient required to force liquid through the tube at the rate observed would be much greater than that which is likely to occur. Both light and electron microscopic evidence suggests that such obstructions in the form of protein fibrils ("P protein") occur both in the lumen of the sieve tube and in the pores of the perforated baffles (sieve plates) which occur at frequent intervals along its length. Unfortunately the evidence from microscopic studies does not unequivocally establish the condition of the sieve tube in the normal functional condition and proponents of the pressure flow hypothesis contend that the apparent blocking of sieve tube

lumen and sieve plate pores with P protein is an artefact arising from the release of pressure which occurs when the material is being prepared for microscopic observation.

Spanner rejects this argument (*Nature*, **232**, 157; 1971) and believes that the pressure flow mechanism is untenable because of the impossibly high pressure gradients which would be required to force liquid through partly obstructed tubes. He has suggested that mass flow through the sieve tubes is brought about by an electro-osmotic mechanism operating across the sieve plate. Thus the sieve plates have a vital role in boosting flow at intervals along the transport pathways instead of being a hindrance as they are to the pressure flow mechanism.

The electro-osmotic mechanism was criticized by Dr E. A. C. MacRobbie (University of Cambridge) on the grounds that the fluxes of potassium ions required to maintain the necessary electrical gradient across the sieve plate in the manner proposed by Spanner would be several orders of magnitude greater than those normally found in living cells, and would be beyond the energetic capability of the cells concerned. She put forward an alternative hypothesis similar to that recently advocated by a Cambridge colleague, F. B. P. Wooding. Wooding has proposed (*Phloem* (Oxford Biology Readers, No. 15); Oxford University Press, 1971) that longitudinal movement of solution in the sieve tubes may be brought about by rhythmic undulations of P protein fibrils. Contraction and relaxation of protein fibres have already been implicated in the circulation of cytoplasm in some algal cells and in fungal filaments. There is some evidence that P protein fibres can be induced to contract by ATP in the same way as muscle fibres and flagellae, but further biochemical studies of P protein fibres are required before much credence can be given to this hypothesis.

The contractile fibre mechanism has a good deal in common with the proposal of R. Thaine that transport in sieve tubes occurs through "transcellular strands" by peristaltic pumping caused by contraction and relaxation of protein constituents in the walls of these strands. Dr Thaine was unable to be present at the meeting but Dr D. Aikman (University of East Anglia) presented some calculations which indicate that this mechanism is energetically quite feasible. In spite of the recent observations of Jarvis and Thaine (*Nature New Biology*, **232**, 236; 1971) most plant physiologists remain sceptical about the reality of transcellular strands. Elucidation of the structure of functional sieve tubes is required before any one of the current hypotheses can be supported.