

cellular and transcellular routes for  $K^+$  redistribution remain uncertain. The present results provide evidence that the  $K^+$  flux associated with a voltage gradient in brain tissue is mainly transcellular.

A voltage gradient in the extracellular space will cause fluxes of all the ions present, in proportions which depend on their various mobilities and concentrations. The proportion of the electric current carried by  $K^+$  (the  $K^+$  transport number) should be approximately 0.012 unless the extracellular fluid differs substantially from cerebrospinal fluid. The  $K^+$  transport number for current flowing through cells should be higher than this figure (particularly for glial cells) because of the relatively high membrane conductance for  $K^+$  compared with other ions. Thus measurement of the  $K^+$  transport number for bulk brain tissue can provide information about the routes for  $K^+$  movement.

$K^+$  fluxes across the pial surface have been measured for steady currents passed through the brain, from a chlorided silver wire in a cup on the neocortical surface to an indifferent electrode in neck muscle. Urethane-anaesthetized rats were used. The cup (5 mm diam.) was initially filled with saline (130  $\mu$ l.: 140 mmol/l NaCl, 3–3.5 mmol/l KCl), and was constantly stirred. Changes of  $[K^+]$  in the cup were measured either by removal of the contents for flame photometry, or by continuous monitoring with a  $K^+$ -sensitive electrode. Typically a current of 0.1 mA (0.5 mA/cm<sup>2</sup>, producing a maximum voltage gradient approximately 12 mV/mm in the brain) might be passed in either direction for 400 sec. The  $K^+$  flux (volume  $\times$  rate of change of  $[K^+]$ ) rose approximately exponentially after current onset ( $\tau = 100$ –150 sec), reaching steady levels corresponding to transport numbers of 0.05–0.08. The exponential lag may be attributable to diffusion through the superficial layers of tissue. Potassium released by activation of nerve cells did not appear to contribute directly to the results, since a regime in which the direction of current was reversed every 100 msec did not produce detectable changes of  $[K^+]$  in the cup, though it probably activated the cells more effectively than steady currents.

The high measured  $K^+$  transport numbers (4 to 6 times higher than in e.c.f.) suggest that at least 75% of the  $K^+$  flux produced by a potential gradient may pass through cells.

I am grateful to D. M. Band and T. Treasure of St Thomas's Hospital Medical School for providing  $K^+$ -sensitive and reference electrodes.

#### REFERENCE

- ORKAND, R. K., NICHOLLS, J. G. & KUFFLER, S. W. (1966). *J. Neurophysiol.* **29**, 788–806.

#### The migration of potassium produced by electric current through brain tissue

By A. R. GARDNER-MEDWIN. *Department of Physiology, University College London, London WC1E 6BT*

When there is an electrochemical gradient for potassium ions in the extracellular space of the brain, there is a net flux of  $K^+$  through the tissue. It is a controversial point whether this flux takes place mainly through intercellular clefts or through the membranes and cytoplasm of glial and nerve cells. Orkand, Nicholls & Kuffler (1966) pointed out that the high  $K^+$  permeability and electrical junctions of glial cells may permit transcellular  $K^+$  fluxes; but the relative contributions of extra-