could be recorded in human subjects by means of surface electrodes, limb leads and a capillary electrometer. The further development of electro-cardiology was made possible by the introduction of the quartz fibre galvanometer (Einthoven, 1912, see demonstration by Adrian, Channel, Cohen & Noble, p. 67P).

The apparatus includes a contemporary capillary electrometer, rails and trolley for the photographic plate which was made to run horizontally by a weight and clockwork mechanism, a separate capillary and photo-graphic recorder with a rotating drum and records obtained with the electrometer.

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A capillary electrometer

BY F. W. CAMPBELL and D. PELLI. Physiological Laboratory, Cambridge University

The capillary electrometer was developed by Lippman in 1873 to make the first measurements of the relations between surface tension and polarizing potential at a bilayer (Overbeek, 1952). Adrian's instrument (see Fig. 1), essentially the same as Lippman's, was used to make records of small changing voltages by casting the shadow of the column of mercury upon moving bromide paper.

Mercury and an electrolyte (dilute sulphuric acid) meet in a fine capillary. The bilayer acts as a capacitor which is charged by the applied voltage. The accumulated + or − charges repel each other, tending to make the surface expand, thus reducing the surface tension.

The surface tension, γ, is related to the applied voltage, V, by

$$\frac{\delta\gamma}{\delta V^2} = C,$$

where the capacitance, C, is a complicated function of the voltage, V. For small V (peak to peak < 100 mV) this is approximately

$$\gamma \sim \gamma_0 - C_0 E_0 V,$$

where C_0, γ_0 and E_0 are constants. Since $E_0 \gg V$, a term in V^2 has been dropped.

The driving pressure resulting from the surface tension is opposed by the pressures resulting from the weight of the column, viscous drag and

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inertia. This is a second-order linear system. The undamped resonant frequency, W, is determined by the familiar pendulum equation:

$$\frac{W}{2\pi} = \frac{1}{2\pi}\sqrt{\frac{g}{L}} \sim 2{\cdot}2 \text{ Hz},$$

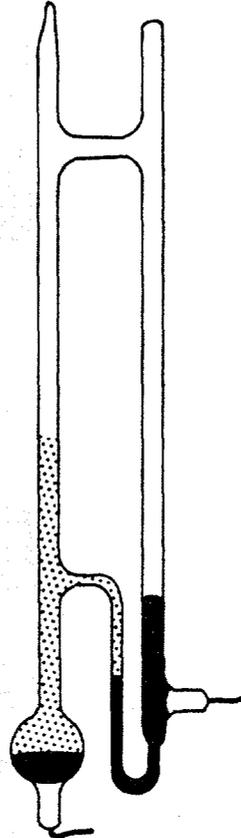where L is the length of tube which contains mercury, about 5 cm in Adrian's device.

Fig. 1. A capillary electrometer. The black represents mercury. The dotted area indicates dilute sulphuric acid. The two tungsten wires allow electrical connexion.

We have measured the frequency response of the capillary electrometer. The data are plotted on a log–log Bode plot in Fig. 2. Lines with slopes of 0, −1, and −2, were fitted by eye. They indicate an undamped resonant frequency of about 2 Hz, in agreement with the calculation.

The complete transfer function represented by the lines is

$$\frac{1}{(S + (2\pi)\ 0{\cdot}6)(S + (2\pi)\ 3{\cdot}0)}.$$

Lucas (1912) made a machine to correct the records made from the capillary electrometer. The user inputs the abscissa, ordinate, and slope

of each point. The machine, using gears and levers, realizes the transfer-function
$$(S + W_0),$$

and outputs a new graph. By setting $W_0 = (2\pi)\ 0\cdot 6$ and operating the machine, a new graph is created, related to the original by the transfer function

$$(S + (2\pi)\ 0\cdot 6) \times \frac{1}{(S + (2\pi)\ 0\cdot 6)(S + (2\pi)\ 3\cdot 0)} = \frac{1}{(S + (2\pi)\ 3\cdot 0)}.$$

While this is a fivefold increase ($3\cdot 0/0\cdot 6$) of the useable frequency range, it is surprising that Lucas makes no mention of using the machine a second
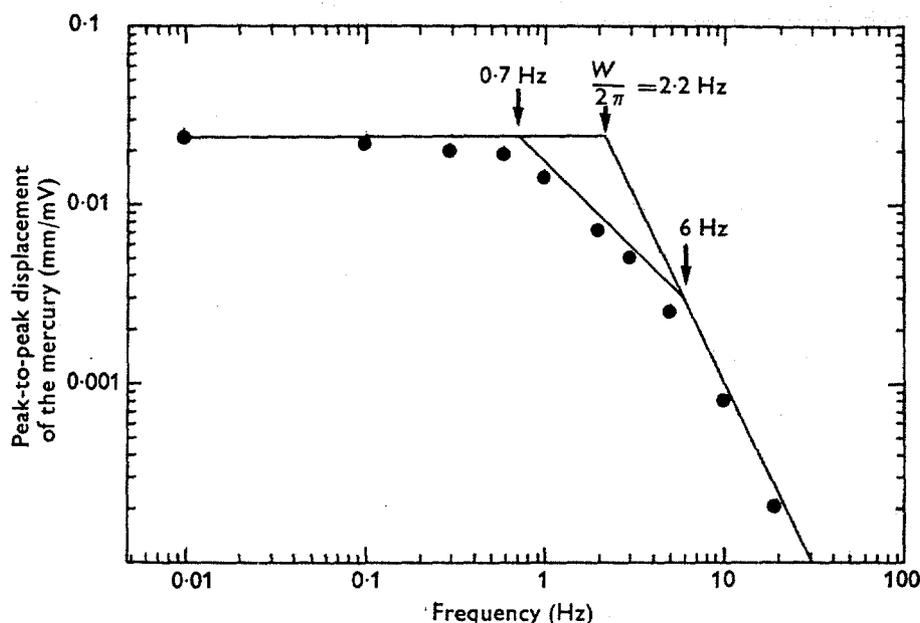

Fig. 2. A log-to-log-Bode plot of the frequency response of Adrian's capillary electrometer. The straight lines represent the transfer function:

$$\frac{0\cdot 084\ \text{mm/mV}}{(S + (2\pi)\ 0\cdot 6)\ (S + (2\pi)\ 3\cdot 0)}.$$

time, to completely correct the response. Of course, frequencies higher than 10 Hz will be so attenuated as to be lost before input into the machine anyway.

A simpler way of improving the response would be to reduce the length of mercury which has to move; a threefold improvement in frequency response should be easily attainable.

Both Adrian's capillary electrometer and Lucas's machine were demonstrated. Fig. 1 A and B of the following demonstration showed records made with a capillary electrometer by Waller (1887).

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The Einthoven string galvanometer and the interpretation of the T wave of the electrocardiogram

BY R. H. ADRIAN, R. C. CHANNELL, I. COHEN and D. NOBLE. *The Physiological Laboratory, Downing Street, Cambridge, and the University Laboratory of Physiology, South Parks Road, Oxford*

The flow of electric current during the heartbeat was first demonstrated in 1856 by Kölliker and Müller. They placed a frog nerve–muscle preparation in direct contact with the ventricle and were able to show that there are two distinct electrical changes during each contraction of the ventricle. The origin of the second of these changes (which, following Einthoven, is called the T wave) has remained controversial to the present day.

The first recordings showing the magnitudes and directions of the components of the electrocardiogram were obtained using the capillary electrometer (see demonstration by Campbell & Pelli, 1976) and the first accurate analysis was performed by Burdon-Sanderson & Page (1880). Waller (1887) first used this method to record from the surface of the human body. The currents at the surface of the body were, however, too weak to allow good recordings to be obtained with this instrument (Fig. 1*A*). An example of the degree of resolution that could be obtained under more favourable conditions is shown in Fig. 1*B*, which is a record obtained by Gotch (1910) from electrodes placed directly on the surface of the heart of a tortoise. The currents are then much stronger and the events occur more slowly in this case than in mammals (2·5 sec per cycle as opposed to less than 1 sec per cycle). There is clear resolution between the two waves corresponding to ventricular activity. This record is interesting in showing the second wave occurring in the opposite direction (negative) to the first (positive). This is the result expected when the excitation travels as a wave of constant duration from base to apex, and in this it corresponds to the simple diphasic wave obtained extracellularly from nerve or muscle (see Fig. 1*C*).
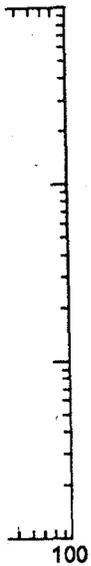
In 1892 Bayliss and Starling showed that in the mammalian heart the second wave of the record obtained from the surface of the body is in the *same* direction as the first (i.e. the T wave is positive). They explained the phenomenon by supposing that the excitation lasts longer at the base than at the apex.