



Fig. 2. Pressure-volume diagram of the lungs. Broken line (—○—), static recoil curve of the lung, obtained from pleural pressures during breathholding. Circles are experimental points averaged over pressure excursion with the heart beat at each volume. Continuous line shows pressure swings caused by heart beat: pleural pressures were recorded during one slow and maximal expiration, while producing a soft and constant tone on a recorder at maximum inspiration. TCL = total lung capacity. RA = residual volume. Dashed loop (— — —), average pressure-volume loop during inspiration (left limb) and expiration (right limb) at controlled flow rates (see \dot{V} recording in Fig. 1).

airflow is small, and to measure viscous resistive pressures adequately requires relatively high flow rates (much higher than those needed for tone production on the recorder). Devices to achieve such higher constant flow rates have been used by Mead and by Allander *et al.* (4). Their flow regulators keep airflow rate constant, regardless of subject effort. The present method, on the other hand, provides the subject with an audible signal which helps him to regulate his own effort in order to maintain a constant flow rate. The higher flow rates needed for resistive pressure measurements can be obtained by placing a leak parallel with an inspiratory and expiratory recorder (Fig. 1) (5). A Fleisch flow-meter records total flow rate. The total flow is divided into flow through the leak and flow through one of the two recorders connected to both sides of a low-resistance breathing valve. The inspiratory recorder (above the valve in Fig. 1) is inverted; it is placed in a tube with only the mouthpiece open to atmosphere. This recorder produces a tone when the subject inspires at a sufficiently high flow rate. The other recorder is connected to the expiratory side of the breathing valve

and sounds during expiration. The size of the leak determines the total airflow rate at which both recorders will sound. The choice of total flow rate is a matter of compromise: it should be large enough to require measurable resistive pressures and small enough to be maintained over most of the lung volume. In practice we used total inspiratory plus expiratory flow rates of 2 to 3 liters/sec for healthy subjects. The \dot{V} record in the lower part of Fig. 1 illustrates the constancy of flow rates. Pressure-volume loops recorded during such constant flow breaths are shown in Fig. 2. The loops are displaced to the left of the static recoil curve because inspiratory flow rate is larger than expiratory flow rate (see flow curve in Fig. 1). This difference is caused by a slight difference between the resistances of the inspiratory and expiratory parts of the breathing circuit. The resistive pressure required for the sum of inspiratory and expiratory flow rate can be read from the diagram as the horizontal distance between the inspiratory (left) and the expiratory (right) limbs of the loop. Pulmonary viscous resistance can then be calculated as the ratio of resistive pressure to flow rate. At the flow rate used for the dynamic P - V loops, the slope of both limbs of the loop differs from the slope of the static lung recoil curve. Apparently, dynamic compliance is lower than static compliance in this subject. Such changes in the slope of P - V loops with increasing flow rates, if they occur, demonstrate that compliance is dependent upon breathing frequency (6). Preliminary experiments have shown that these constant-flow P - V loops demonstrate the bronchoconstrictive effect of an inhaled histamine aerosol on the airways by an increase of resistive pressure, at equal flow rates, and by an increased frequency-dependence of lung compliance.

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References and Notes

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2. J. Milic-Emili, J. Mead, J. M. Turner, E. M. Glauser, *ibid.*, p. 207 (1964).
3. Technical details of the methods used are discussed in a previous paper by A. Bouhuys, D. F. Proctor, J. Mead, *J. Appl. Physiol.* **21**, 483 (1966), which also contains a discussion of the pressure-volume diagram and its interpretation during singing. The mechanical events in producing tones on a recorder are similar to those during singing. In general, driving (subglottic) pressures are higher, and flow rates are more variable, during singing.

4. J. Mead, private communication; C. Allander, S. Ingelstedt, B. Jonson, H. Westling, *Med. Exper.* **11**, 253 (1964).
5. This principle was introduced by De Bono for measurements of peak expiratory flow rates with a whistle; E. F. De Bono, *Lancet* **1963-II**, 1146 (1963).
6. A. B. Otis, C. B. McKerroy, R. A. Bartlett, J. Mead, M. B. McIlroy, N. J. Selverstone, E. P. Radford, Jr., *J. Appl. Physiol.* **8**, 427 (1956).
7. I thank Dr. Björn Jonson for the discussions on the flow-regulators of Allander *et al.* (4) which led to the present study. Supported by PHS grant OH-00207.

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Reversal in Tactile and Visual Learning

Our conclusion [*Science* **153**, 205 (1966)] that tactile and visual learning take place in independent functional systems was based on results of experiments in which monkeys were required to make tactile and visual object discriminations. Biederman refers to work [*Science* **154**, 677 (1966)] with rats and spatial discriminations. We are not certain how closely one can compare results obtained with these two different species and discriminations. We know of no work that shows an increase of the reversal-learning score by the monkey with overtraining of original learning for tactile object discriminations.

Furthermore, Biederman's argument applies only to our control ratio of 75:1, relating to original and reversal learning by touch. However, our conclusion was based upon two separate lines of evidence: first, the small reversal ratio across modalities when compared with the large reversal ratio within one modality; and, secondly, the good performance of our animals during 80 test trials in the light and dark. Biederman's point cannot bear upon either the small reversal ratio across modalities of 1.6:1 or upon the good performance during the 80 test trials. Finally, we cannot agree with him that original learning light and reversal in the light would have provided either helpful or necessary evidence: because our experimental animals were originally trained in the dark, it was useful only to compare dark-to-light reversal (experimental) with dark-to-dark reversal (control)—which we did.

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