MECHANISMS ENSURING THE OPTIMAL EFFICIENCY OF RESPIRATION

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Some hypotheses regarding the method of securing optimal (reducing the work of the respiratory musculature to a minimum) efficiency of respiration in living organisms were tested experimentally. In experiments on rabbits an artificial feedback system was used, in which the resistance to inspiration depended on its duration. By changing the characteristics of the feedback circuit, the conditions under which the optimum was reached could be altered. The experiments showed that the optimum is attained through comparatively slow variations in the static characteristic of the respiratory system, determining the relationship between the parameters of respiration and resistance to it. The experiments did not confirm the hypothesis of a continuous (from inspiration through to inspiration) search for the optimum by the respiratory system.

The view is held that the parameters of external respiration (frequency, depth, and so on) are established by the respiratory system so that, for a given volume of ventilation, the work of the respiratory musculature is minimal. This hypothesis has become widely accepted [6].

An increase in the resistance of respiration causes marked changes in the parameters of respiration [2, 7]. In particular, the duration of inspiration is increased. In a previous investigation [4] the author showed that changes in the parameters of respiration immediately after the introduction of resistance depend quantitatively on the magnitude of the resistance. The greater the resistance, the more prolonged the inspiration. Other experiments (unpublished data) have shown that these conclusions apply also to the parameters of the quasi-stabilized pattern of respiration observed 10-20 respiratory cycles after introduction of the resistance. These changes in the pattern of respiration can be explained by adaptation of the system to the changed conditions, with readjustment to a new optimum. This optimum may be either the minimum of work during respiration [8, 9] or a compromise between it and the "essential" volume of ventilation [5]. This hypothesis of optimization of the pattern of respiration raises the question of how this adjustment to the optimum takes place. It is frequently taken almost for granted that this adjustment is effected through a continuous search and adaptation to external conditions [3, 10].

However, the changes observed in respiration can also be explained on the assumption that during evolution certain "rigid" functional relationships determining the magnitudes of the parameters under various external conditions have been developed, and these ensure the most efficient pattern of respiration. They may also be explained by a compromise: the general character of this functional relationship has developed in the course of evolution, that its precise form, ensuring optimal conditions of respiration, is subject to continuous selection. These hypotheses both demand experimental verification, and the investigation described below was carried out for this purpose.

The verification can be carried out as follows. Let the animal be placed in experimental conditions under which the resistance to respiration depends on one of the parameters of respiration (in this investigation, the duration of inspiration was chosen as that parameter). This can be done by means of an arti-

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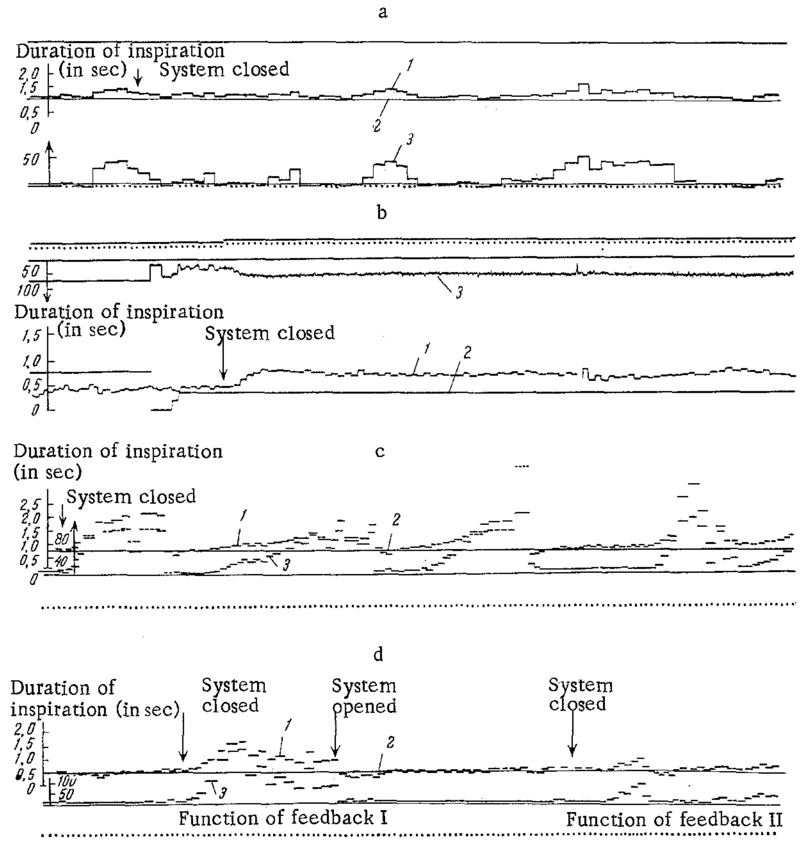

Fig. 1. Changes in duration of inspiration in rabbits in a closed system with type 1 feedback. Ordinates of each "step" in curve 1 are proportional to the duration of inspiration in the previous respiratory cycle. Scale of curve 1 shown on left of records; 2) zero line for curve 1; 3) change in resistance to inspiration (scale of resistance shown in mm water/2 liters/min). Time marker 1 sec. a) Pattern 1; b) pattern 2; c) "intermediate" pattern with changes from pattern 1 to pattern 2 and vice versa; d) "imposed" transition from pattern 2 to pattern 1 with a change in gradient of the characteristic of the feedback element. On the left: feedback characteristic is such that with an increase in the duration of inspiration by 0.5 sec, resistance is increased by 100 mm water/2 liters/min; on the right; by 20 mm water/2 liters/min.

ficial feedback. In such a closed system, the values of the parameters corresponding to optimal conditions will differ, generally speaking, from the "normal" values. By changing the characteristics of the feedback system, the optimal values of the parameters can be changed at will. If under these conditions the animal appeared to "find" the optimal (for the given characteristic of the feedback) parameters rapidly (in the course of a few respiratory cycles) every time, this would confirm the first (adaptation) hypothesis. If, on the other hand, the parameters of respiration established in the closed system were not determined by their optimal values, but by the conditions of static equilibrium of the closed systems [1], this would be evidence in support of the second (evolutionary) hypothesis.

EXPERIMENTAL METHOD

Rabbits were chosen as experimental animals. The apparatus for creating a resistance to inspiration and for measuring the parameters of respiration was described briefly in an earlier paper [4]. A signal proportional to the duration of inspiration [4] was applied to the input of a functional transducer acting as the feedback element; the voltage at its output determined the magnitude of the resistance. Depending on the chosen characteristic of the feedback, the resistance to inspiration was increased (type 1 feedback) or decreased (type 2 feedback) with an increase in the duration of inspiration. Depending on the shift applied

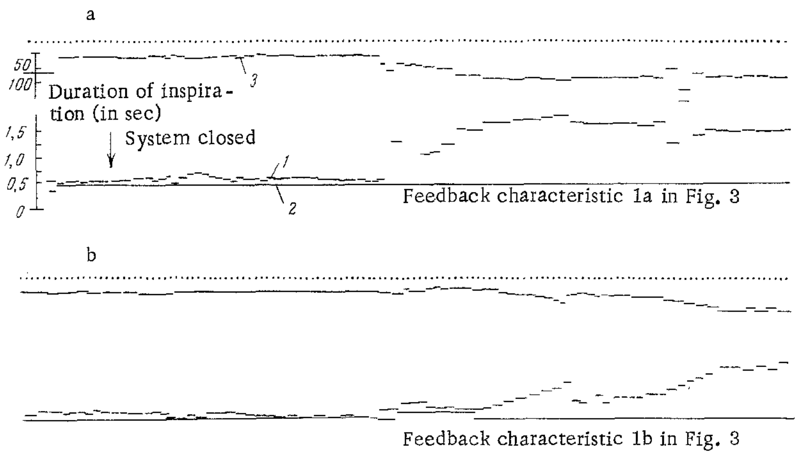

Fig. 2. Changes in duration of inspiration in rabbits in a closed system with type 1 feedback (verification of agreement between observed and calculated patterns): a, b) fragments of one continuous record obtained by experiment. 1) Curve of duration of inspiration of a rabbit; 2) duration for which resistance to inspiration is 0 (in agreement with feedback characteristic); 3) curve of change in resistance to inspiration (scale of resistance shown in mm water/2 liters/min). Time marker 1 sec. Displacement of line 2 in fragment b indicates moment of change of feedback characteristic (feedback characteristics used in this experiment are shown in Fig. 3).

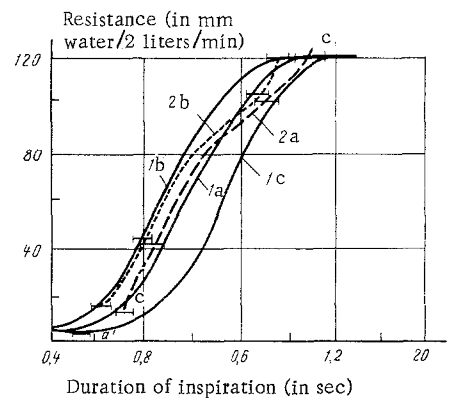

Fig. 3. Calculation of patterns of respiration in closed system. Continuous lines show feedback characteristics, broken lines static characteristics of animal. 1a, 2a) Feedback characteristic and static characteristic of animal before closure of system; 2b) static characteristic of animal recorded after spontaneous change in pattern of respiration (beginning of fragment b); 1b) feedback characteristic changed (see fragment b).

to the functional transducer, the resistance to inspiration during "normal" inspiration (the "origin" of the feedback characteristic) was altered. The apparatus permitted opening of the system, i.e., allowed the resistance to be changed from an external, independent source. This was necessary whenever it was required to obtain a static characteristic of the animal, i.e., when the duration of inspiration under established conditions was dependent on the magnitude of the resistance. The duration of inspiration and, in some cases, the magnitude of the resistance were recorded continuously during the experiment on a loop oscillograph. A more detailed account of the apparatus and experimental method can be found in an earlier paper [5].

EXPERIMENTAL RESULTS

With a type 1 feedback in the closed system, two principal patterns of respiration were observed. In pattern 1, the duration of inspiration was unchanged after closure of the system, while in pattern 2 the duration of inspiration increased sharply (along with the resistance) after closure of the system. Which pattern was found depended essentially on the characteristic of the feedback element (its gradient, shape, and displacement). For example, increasing the gradient invariably led to a change from pattern 1 to pattern 2. With certain characteristics, regular changes from pattern 1 to pattern 2 and vice versa were observed. Examples of the records obtained in the experiments are shown in Fig. 1.

The results show that in a closed system the duration of inspiration did not correspond to the optimal pattern of respiration. For example, in pattern 2 the work of respiration was significantly higher than the possible minimum: a decrease in duration even to the initial level would sharply reduce the resistance to inspiration and, correspondingly, the work of respiration. Consequently, the "adaptation" hypothesis was not valid under the conditions of a changed resistance.

To test the "evolutionary" hypothesis, immediately before the experiment with a closed system the static characteristic of the animal was recorded. Knowing this characteristic, and also that of the feedback element, while determining the point of intersection of the characteristics and their stability, the possible conditions in the closed system could be found. The points of intersection determined in this way were found to predict the duration of inspiration in the closed system with an accuracy of 0.05-0.1 sec (for both types of feedback). The pattern of respiration could be predicted with equal accuracy when arbitrary changes were made in the feedback characteristic. When spontaneous changes took place in the duration of inspiration, the animal's static characteristic was changed; the new pattern of respiration then corresponded with the previous accuracy to the "calculated" pattern. Fragments of the same record, obtained in an experiment with type 1 feedback, are shown in Fig. 2. Both spontaneous and imposed changes, i.e., those due to a change in the feedback characteristic, in the patterns can be seen. The feedback characteristics and static characteristics of the animal recorded during this particular experiment are given in Fig. 3. Comparison of the patterns of respiration in Fig. 2 and the calculated values (points of intersection in Fig. 3) demonstrates the agreement between calculation and experiment.

The results of these experiments thus showed that the respiratory system is unable to search continuously (from inspiration to inspiration) for the optimal (as regards the work of respiration) pattern of respiration and the actual parameters of respiration are determined by external conditions in accordance with the functional relationship established in the given animal.

In 70% of cases, slow (measured in minutes) spontaneous changes in the pattern in the closed system led to a decrease in the resistance to inspiration. This fact suggests that the animal is able to make a slow search for the optimal pattern by adapting its static characteristic to the changed environmental conditions.

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