LONG-LASTING CHANGES IN MOTOR ACTIVITY PRODUCED EXPERIMENTALLY IN CHICK EMBRYOS

O. V. Bogdanov, A. A. Smetankin,
and V. V. Ved'

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Long-term modification of motor activity of chick embryos was shown to be inducible under controlled experimental conditions. Characteristic time periods were distinguished during controlled reinforcement of movements by electric shocks of threshold amplitudes: intermediate periods, periods of stable modification of motor activity during minimization of the number of electric shocks, and periods of aftereffect. It is concluded that the single adaptive effect (minimization of biologically adverse influences) is due to structural and temporal reorganizations of the biorhythm of motor activity with selective enhancement of components not reinforced by adverse influences.

KEY WORDS: adaptive self-regulation; endogenous biorhythms.

Recent investigations have shown the transformation of motor activity of chick embryos from predominantly self-regulated, in the early stages of development, to a reflex-controlled type incorporating supraspinal influences [1, 4]. The study of adaptive changes in movements of the embryo during this period and investigation of the mechanisms responsible for them under controlled experimental conditions [2], with the formation of new states by the use of suitably chosen conditions, which would directly indicate the adaptive character of the oriented changes in movements, is a matter of considerable interest.

EXPERIMENTAL METHOD

Experiments were carried out on 50 18-19-day chick embryos with a controlled decrease or increase in the amplitude of their spontaneous motor activity (25 embryos in each group). The results of 26 experiments (13 on each group) were subjected to statistical analysis. The basic techniques were described previously [3]. The assigned threshold of motor activity was displayed on the output system of an analog computer. With a change in the momentary mean amplitude of the movements (the "envelope") above or below the threshold (depending on the assigned conditions) electrical stimulation of the skin in the dorsal region of the embryo was automatically applied and was switched off when motor activity reached subthreshold levels. Each experiment consisted of two cycles of experimental stimulation and one control cycle, when reinforcing electric shocks were applied to the embryo at random time intervals, and background recording periods before and after each stimulation and control cycle. The duration of each cycle was regulated by the maximal number of reinforcements (reinforcement stimuli or pseudostimuli in the background period), namely 1000. Square pulses with a frequency of 10 Hz, a duration of 1 msec, and an amplitude of 300 to 500 mA were used as electrodermal reinforcement (the magnitude of the electric shocks was chosen individually for each embryo and were always 10% below the value evoking a reflex motor response to single stimulation).

EXPERIMENTAL RESULTS

The experimental results showed that self-controlled electrical stimulation leads to changes in motor activity of the embryos in the direction resulting in a stable reduction in the number of reinforcements (Fig. 1A, B, II). This relationship was found to be universal and common to the control regimes of both an increase and a decrease in amplitude of the embryonic movements. Accordingly it was possible to judge the success of the result of con-

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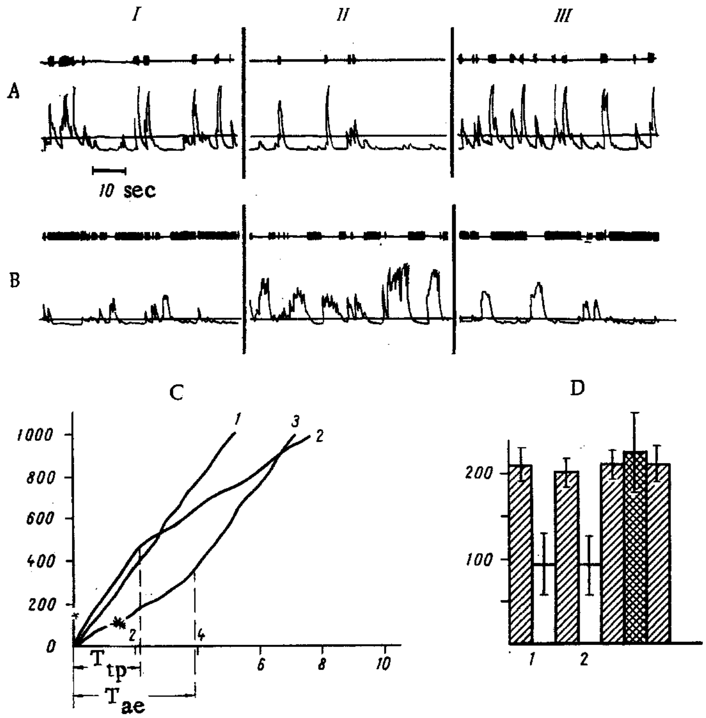

Fig. 1. Fragments of records of motor activity of 19-day chick embryos during controlled experiment (A, B), differentiation of periods of stable minimization of self-reinforcements (C), and dynamics of reinforcement stimuli during controlled stimulation (D). A) Regime oriented toward decrease, B) toward increase in amplitude of movements. I) Background (pseudostimulation); II) at fifth minute of controlled stimulation; III) at fifth minute of aftereffect (pseudostimulation). From top to bottom, marker of stimuli (II) and pseudostimuli (I, III), and momentary mean (envelope) of movements; straight line on "envelope" of movements represents activation threshold of stimulation; C) typical function of cumulative total of reinforcement stimuli. 1) Background; 2) controlled stimulation; 3) aftereffect. Abscissa, time (in min); ordinate, total number of reinforcement stimuli at each moment of time. T_{tp}) Duration of transitional period, T_{ae}) duration of period of aftereffect; D) abscissa, experimental cycles [oblique shading indicates cycles of pseudostimulation; no shading, cycles of stimulation oriented toward decrease (1) and increase (2) of motor activity; cross-hatching indicates uncontrolled stimulation]; ordinate, mean number of stimuli per minute.

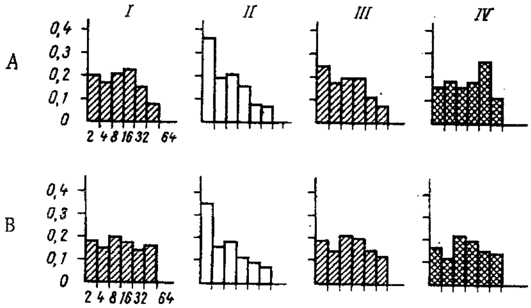

Fig. 2. Temporal redistribution of reinforcement stimuli in regime oriented toward increase (A) and decrease (B) in motor activity. I) Volley histograms of pseudostimuli in background, II) of reinforcement stimuli during periods of stable reorganization of movements, III) after restoration of movements, IV) during uncontrolled stimulation. Abscissa, number of stimuli in volley of reinforcement; ordinate, relative proportion of volleys with a particular number of stimuli in them.

trolling the embryos' motor activity primarily from the change in the character of distribution of the electrical reinforcement stimuli for an assigned level of movements during controlled stimulation relative to the background distribution. For this purpose, in each experiment the function of the cumulative number of reinforcement stimuli was plotted for all cycles. A typical example of this function in the background and during controlled stimulation is shown in Fig. 1C. Since the analytical relationship was so comparatively simple, it was found that the number of reinforcement stimuli per unit time was greatest in the first minutes during the cycles of controlled stimulation (transitional periods). On withdrawal of the self-reinforcements, the rate of accumulation of pseudostimuli gradually increased up to the background level (periods of aftereffect). During the remaining time intervals in the background and during self-reinforcement the rate of accumulation of reinforcement or pseudoreinforcement stimuli changed only very slightly with a marked decrease in the number of self-stimulations. In the last case, this function could be approximated by the method of regression analysis to a linear function in 81% of cases, with a confidence interval of 95%. This result quantitatively suggests constancy of the rate of accumulation of self-reinforcement stimuli while these were decreasing, compared with the background, and accumulation of pseudostimuli in the background period. The constant rate of accumulation of pseudostimuli in the background and of reinforcement stimuli during controlled stimulation suggests the existence of different steady states of motor activity in these periods. In the transition periods, from 1 to 3 min in duration (Fig. 1C), an increase in scatter of amplitude of the movements and in the chaotic character of alternation of high- and low-amplitude movements (nonsteady state) was observed in both control regimes. The periods of aftereffect, lasting from 2 to 6 min (Fig. 1C), were characterized by gradual restoration of spontaneous motor activity. Analysis of reinforcements during cycles of controlled stimulation showed that in 11 of 13 embryos, oriented to a decrease in movement amplitude, minimization of self-reinforcements occurred. The number of reinforcement stimuli fell for both groups on average by 2.07 times ($P < 0.001$) compared with the background (Fig. 1D). The decrease in the number of reinforcements per unit time was accompanied by a significant temporal redistribution (Fig. 2A, B). Volleys of reinforcement, with 8-16 stimuli per volley, most frequently encountered in the background period, were replaced during controlled stimulation by shorter volleys, with two to four stimuli per volley. The same relationship was found for both control regimes.

Analysis of the data on motor activity showed a considerable change in amplitude of the movements during the period of stable minimization of the number of reinforcement stimuli. The amplitude of the movements increased on average by 24% ($P < 0.001$) during reinforcement of low-amplitude components and decreased on average by 31% ($P < 0.001$) during reinforcement

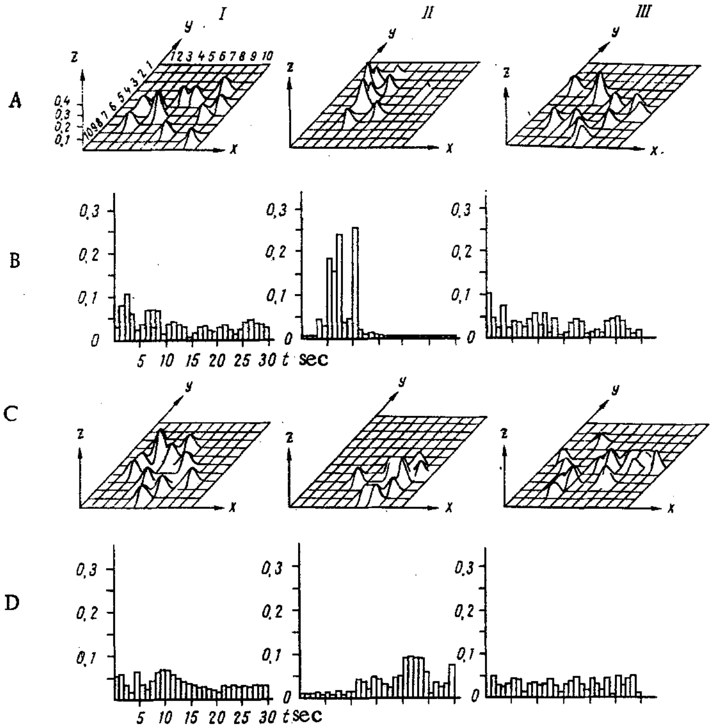

Fig. 3. Changes in structure of motor activity of two 19-day chick embryos during controlled stimulation with control oriented toward a decrease (A, B) and an increase (C, D) in amplitude of movements. A, C: along x axis) mean amplitude of single complexes of movements in each successive 30-sec time cut; along y axis) number of separate complexes of movements; along z axis) frequency of occurrence of 30-sec time cuts with an assigned number of single complexes of movements and with an assigned mean amplitude of these complexes; B, D: abscissa, periods of harmonic components of motor activity (in sec); ordinate, relative proportion of harmonics of a particular period.

of the high-amplitude components of motor activity. Changes in the temporal and amplitude structure of the motor complexes were observed at the same time (Fig. 3A, C). In the regime of reinforcement of low-amplitude components of movements an increase in the number of movements per unit time and in their mean amplitude was observed. In the regime of reinforcement of high-amplitude components of the movements a decrease in the number of movements per unit time and, correspondingly, in their mean amplitude was observed.

The periods of stable minimization of the number of reinforcement stimuli in the control cycles were characterized by changes in the slow modulating rhythms of motor activity (Fig. 3B, D). Whereas in the background the motor activity of the embryos was characterized by a virtually uniform distribution of harmonic components of different periods (from 1 to 30 sec), during controlled stimulation periods of a certain duration began to predominate: in the regime of orientation toward a decrease in amplitude of the movements harmonics with a period of 5-11 sec predominated, whereas in the regime oriented toward an increase, those with a period of 18-25 sec predominated.

Analysis of the results thus showed that the structure of motor activity in periods of stable minimization of reinforcement stimuli, during different regimes of movement control, differs sharply from the background motor activity.

Comparison of the transitional period, period of stable reorganization of motor activity, and the period of aftereffect in repeated cycles of controlled stimulation revealed no significant differences between the first and second cycles.

Control experiments with random stimulation of the embryos showed that under these circumstances the periods described above were absent and there was no decrease in the number of stimuli.

The experimental results thus indicate specific oriented transformations of movements toward the end of embryogenesis in regimes of control oriented in different directions. The single adaptive effect (minimization of stimulating influences) is produced by structural and temporal modifications of the biorhythm of motor activity with a selective enhancement of components not reinforced by adverse (nociceptive) stimulation. This points to the role of endogenous biorhythms as a mechanism of optimization of relations between the organism and its environment [3], which are actively incorporated into adaptive control before the end of embryogenesis in chicks.

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INTERACTION BETWEEN HYPERCAPNIC AND HYPOXIC RESPIRATORY DRIVE DURING MUSCULAR EXERTION

G. G. Isaev

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During the performance of graded muscular exertion against the background of controlled hypercapnia, hypoxia, hyperoxia, and their combinations, the dynamics of the pulmonary ventilation ($\dot{V}$) and the composition of the alveolar gas ($p_a\ CO_2$, $p_a\ O_2$) were investigated in 12 healthy men. The respiratory response was assessed from the absolute values of ventilation at a given value of $p_a\ CO_2$ and from its increase per mm Hg increase in $p_a\ CO_2$ ($\Delta\dot{V}/\Delta p_a\ CO_2$) at rest and on transition to and with establishment of stable conditions of exertion. The respiratory response at the beginning of exertion was accompanied by an upward shift and an increase in the slope of the $\Delta\dot{V}/\Delta p_a\ CO_2$ line, independent of the magnitude of exertion. These changes point to multiplicative ineraction between neurogenic and hypercapnic stimuli with the commencement of exertion. In the steady state of exertion a significant role of the hypoxic stimulus was discovered: During hypoxemia the $\Delta\dot{V}/\Delta p_a\ CO_2$ line was found to be appreciably shifted upward, especially during intensive exertion. This proves that positive interaction between hypercapnic and hypoxic stimuli is potentiated during exertion.

KEY WORDS: regulation of respiration; chemoreceptors; proprioceptors; interaction between respiratory drives; muscular activity.

Complex interaction between the stimuli controlling respiration during muscular activity is still largely unexplained. The importance of chemoreceptive stimuli in the genesis of the neurogenic components of the ventilatory on-response to exertion has recently been demonstrated [1, 5].

The functions of the chemoreceptor apparatus are generally assessed by the response of the pulmonary ventilation to a hypercapnic stimulus. This response is usually measured during rebreathing with CO_2 accumulation. However, this test is difficult to carry out during phys-

Group for Physiology of Respiration, I. P. Pavlov Institute of Physiology, Academy of Medical Sciences of the USSR, Leningrad.

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