DEVELOPMENT OF AUTONOMIC REACTIONS IN FOWLS DURING EMBRYOGENESIS

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The evolution of autonomic reflex reactions in a phylogenetic series of animals has been investigated in this laboratory [2]. The establishment of autonomic reactions in the period of ontogenetic development has been studied in less detail. The information available on this subject [5,6,7] relates mainly to the postnatal period of development of mammals. It has been found that autonomic reactions (particularly those affecting the cardiac activity) to exteroceptive stimuli develop early in postnatal ontogenesis. The changes in autonomic reactions were found to take place in a regular sequence, details of which have been described in different species of animals. It has been concluded [4] from experimental investigations that the hypothesis [9,10], according to which the appearance in the first place of autonomic components during the establishment of orienting and defensive reactions is an adaptive act of preparation for the adequate performance of motor reactions, is correct. This problem has been inadequately studied in relation to the period of embryonic development. I. A. Arshavskii's findings, obtained in the fetuses of mammals whose young are born prematurely, demonstrate the absence of typical pressoreceptor reflexes coordinating the activity of the cardiovascular system; redistribution of the blood as in the case of Loven's reflex is also absent.

It appeared interesting to determine whether a mechanism of unconditioned-reflex regulation of cardiac activity is present in animals born mature, in the period of embryonic development. Fowls undergo such complete development during the intraovular period that at the moment of hatching they are perfectly ready for independent life. We have studied the possibility of obtaining unconditioned-reflex changes in the cardiac activity of the chick embryo during application of exteroceptive stimuli in acute and chronic experimental conditions, and also the possibility of developing a temporary connection with the cardiac activity in the embryonic period.

EXPERIMENTAL METHOD

Acute experiments were carried out on 70 chick embryos from the 7th to the 21st day of development and chronic experiments on 150 chick embryos between the 6th and 21st days of development. The heart rate and motor activity were recorded in the chronic experiments. The technique of the acute experiments has been described previously [3]. In the chronic experiments, while constant temperature conditions were maintained, the heart rate was recorded by means of copper electrodes introduced into opposite ends of the egg. In sterile conditions the shell at the poles of the egg was filed away for an area of 1 mm^2. Copper electrodes, 0.25 mm in diameter, were introduced to a depth of 3-8 mm depending on the age of the embryo, without coming into direct contact with the embryo, and were fixed with phosphate cement. The egg was placed on a stand inside an incubator. The potentials were led to an ac amplifier, manufactured by the Moscow Experimental Factory, and recorded by an ink-writing apparatus.

The stimuli used were a pinprick, pinching the thigh, an electric current of 10 V (acute experiments), and vibration of the egg at 100 cps and an electric current of 3.5-8 V (chronic experiments). In the acute experiments the stimuli were applied in no particular order for a period of 2-4 min, and in the chronic experiments the order was always strictly adhered to: vibration of the egg, electric current, 7-12 stimuli in a period of 2-4 min. The experiment lasted 30-40 min.

The temporary connection was formed after the 14th day of embryonic development in response to a combination of a tone of frequency 2000 cps and intensity 90 dB (the conditioned stimulus) and an electric current of voltage

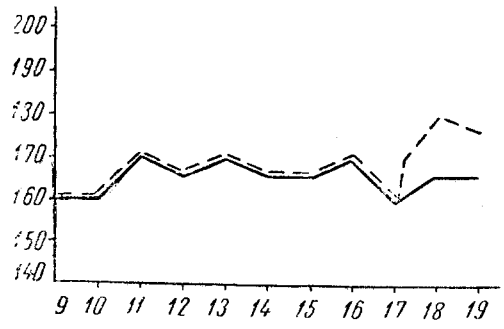

Fig. 1.

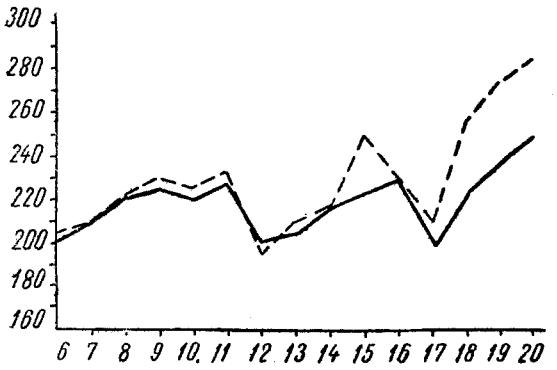

Fig. 2.

Fig. 1. Changes in heart rate during pricking the thigh in acute experiments on chick embryos. Along the axis of abscissas—days of development; along the axis of ordinates—heart rate in beats per minute. Continuous line—background heart rate, broken line—changes in heart rate during application of stimulus.

Fig. 2. Changes in the heart rate during stimulation of chick embryos with an electric current in chronic experiments. Legend as in Fig. 1.

3.5 V and frequency 60 cps (unconditioned stimulus). During the first 1.5-2 days the two stimuli were applied simultaneously at the rate of 7 combinations per day of the experiment. Subsequently, the conditioned stimulus was applied after a delay, gradually increasing to 5 sec, after which the tone and the electric current again acted together for a period of 3-4 sec.

EXPERIMENTAL RESULTS

The preliminary study of the background frequency of the cardiac contractions showed that the heart rate differed significantly in the acute and chronic experimental conditions. In the acute experiments the heart rate remained stable during the experiment. In chronic experimental conditions, observations over a long period (2 h) showed the relatively steady heart rate was transformed into periods of higher and lower frequencies of contraction, the rate remaining relatively constant in the course of these periods. The duration of these periods of relatively stable heart rate varied from 15 to 25 min. In individual cases a gradual rise or fall of the heart rate was observed, without sharp fluctuations.

The application of exteroceptive stimuli in the acute experiments before the 17th day of embryonic development was not followed by any detectable changes in the heart rate, despite the presence of obvious reflex movements (Fig. 1).

After the 17th day of development of the chick embryo changes in cardiac activity could be observed in response to the application of individual stimuli. However, changes in the heart rate were seen in only 15 of the 25 embryos at this stage of development. The reflex changes were characterized by a very slight quickening of the heart rate (by 9-15% of the initial background rate) during pricking and pinching the thigh, and a slowing of the heart rate by 15-19% during stimulation with the electric current. No relationship could be established between the observed changes in cardiac activity and the presence of a motor reaction. Changes in the heart rate during application of the stimuli were inconstant during several applications. Various receptor zones were tested (the beak, forehead, wing, thigh, and foot), but no significant differences were observed in the character of the cardiac reaction.

In the chronic experiments application of the stimuli (electric current, vibration of the egg) caused a slight increase of up to 20-30 beats per minute in the heart rate, or 10-15% of the initial background level; this was inconstant in its appearance and was observed from the 6th day of development (Fig. 2). As a rule, the changes in cardiac activity were preceded by a motor reflex reaction, which persisted despite frequent reapplications of the stimulus. Hence, in the chronic experiments, although the changes in the heart rate were ill defined, they could be seen at a much earlier period of development of the chick embryo. Moreover, they were clearly seen to be connected with the performance of a motor reaction, stressing the nonreflex character of these changes at this particular period of development.

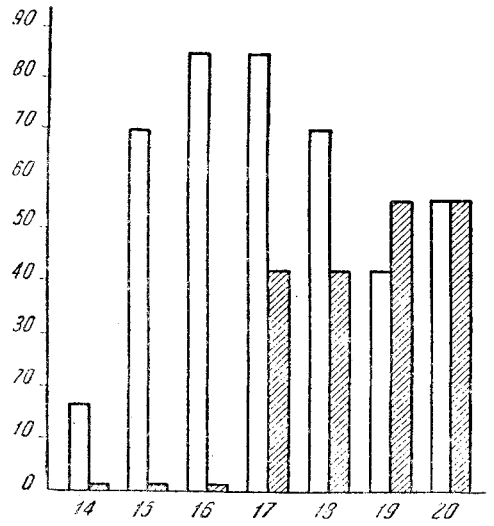

Fig. 3. Dynamics of the formation of a temporary connection in a chick embryo. Along the axis of abscissas—days of development; along the axis of ordinates—percentage of positive responses in experiment. Unshaded columns—temporary motor connections, shaded—autonomic.

After the 17th day of development more marked changes than on previous days were observed in the heart rate in response to application of exteroceptive stimuli. The heart rate varied by 15-20% of the initial background, and the magnitude of these changes became more constant in each experiment. At this period it was difficult to observe a connection between the changes in cardiac activity and the motor reaction; on the contrary, the changes in the heart rate preceded the development of the motor reaction or took place at the same time, thus demonstrating the reflex character of the changes in cardiac activity.

During the application of a single stimuli a very slight increase in the heart rate was observed, followed by the establishment of a lower background level. As a result of summation of a single stimuli a more marked slowing of the background was obtained, returning to its initial level on the day after the experiment. This pattern was reproduced on the 18th day of development. At this age period, after the summation of the action of the single stimuli, the background heart rate rose sharply. The study of the possibility of forming a temporary connection with the cardiac activity showed that from the 14th until the 17th day of embryonic life, only a temporary motor connection could be obtained, in the absence of any changes whatever in the cardiac activity. After the 17-18th day of development a conditioned connection with the cardiac activity could be formed in 66% of the cases (Fig. 3). However, this connection was manifested irregularly from one experiment to the next, and even in the course of the same experiment. The magnitude of the reaction amounted to 8-10% of the initial background level.

The experimental results show that until the 17th day of embryonic development of the chick embryo the regulation of its cardiac activity is in the formative period. The results of the acute experiments demonstrate the presence at this period of a stable background heart rate and absence of changes in the heart rate in response to application of exteroceptive stimuli. In the chronic experiments on the unopened egg, in conditions as near to natural as possible, the stage of formation of cardiac regulation is more clearly apparent. The changes in the relatively constant background value of the heart rate, the changes in the cardiac activity in response to the exteroceptive stimuli before the 17th day of embryonic life, which were directly dependent on the preceding motor reflex reaction of the embryo, and also the impossibility of forming a temporary connection with the cardiac activity are sufficiently clear evidence of this. Unconditioned-reflex regulation of the cardiac activity appears after the 17th day of embryonic development. In the acute experiments changes first appeared in the heart rate at this period in response to the application of exteroceptive stimuli. The character of the changes was also modified in the chronic experimental conditions. Whereas before the 17th day the changes in the heart rate were dependent on the preceding motor reaction, after the 17th day the change in cardiac activity preceded, or appeared at the same time as the motor reaction, thus demonstrating the unconditioned-reflex character of the reaction. Finally, at this period of embryogenesis a temporary connection could be formed with the cardiac activity, thereby demonstrating the considerable widening of the scope of the regulatory powers.

The results show that the character of the development of the regulation of cardiac acitvity in the period of embryogenesis of birds hatching out in a mature state repeats the stages of phylogenesis [8]. The phase of undeveloped regulation (automation) is followed by a phase of marked unconditioned-reflex regulation. Finally, the possibility of regulation by a system of temporary connections appears, forming one type of conditioned-reflex regulation. In conclusion, it must be pointed out that in species which, at the end of embryogenesis, are fully prepared for independent existence, the mechanisms of adaptation to this situation are already formed, so far as the heart is concerned, at this stage. Their degree of development and the character of their manifestation are determined by the ecological properties of the species.

SUMMARY

A study was made of the possibility of obtaining unconditioned reflex shifts in the cardiac activity of the chick embryo in response to exteroceptive stimuli in acute and chronic experimental conditions; a possibility of elaborating a reflex to the cardiac activity during the embryonic period was studied as well. Experimental results indicated that control of the cardiac activity was in the phase of formation up to the 17th day of the chick embryo development. Unconditioned reflex control of the cardiac activity was manifested beginning from the 17th day of the embryonic development. At the same period it is possible to elaborate a temporary reflex to the cardiac activity, which points to a considerable widening of the regulation possibilities by the end of embryogenesis in representatives of birds which hatched mature.

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All abbreviations of periodicals in the above bibliography are letter-by-letter transliterations of the abbreviations as given in the original Russian journal. *Some or all of this periodical literature may well be available in English translation.* A complete list of the cover-to-cover English translations appears at the back of this issue.
