second rat with an earlier version of the present procedure. The abscissa in Fig. 1 covers the 5-minute interval prior to the priming of the apparatus for reinforcement, and is broken down into ten consecutive 30-second periods. The ordinate plots the mean rates of responding during these 30-second periods. The increasing rate of responding that typifies behavior on this schedule of reinforcement results in increasing monotonic curves. The curves drawn through filled circles show the preinjection rates; those through open circles, the postinjection rates. Each pair of curves is an average of the data from the indicated number of sessions. The saline-control curves, being for four sessions prior to any administration of scopolamine, demonstrate that saline causes no disruption. The scopolamine curve shows the typical effect of this drug. In it, responding is depressed, having lost the increasing monotonic pattern normal for this schedule of reinforcement. The curves labeled "saline 1" are for the sessions in which saline was administered after a prior injection of scopolamine, whereas the curves labeled "saline 2" are from sessions with saline when the prior injection had been saline.

The curves show that when saline is administered after scopolamine (saline 1), there is considerable depression of responding, whereas with two consecutive administrations of saline (saline 2) this effect is diminished, although not quite obliterated (*4*). Such a depression of responding by saline may reasonably be termed a placebo effect. This placebo effect does not involve a loss of the monotonic increase in rate during the 5-minute interval. The characteristics of the depression and the manner in which it was brought about suggest, moreover, that it is an example of Pavlovian conditioning. It seems probable that the conditioned stimulus includes the injection of a hypodermic needle into the peritoneal cavity, for mere handling of the animal in several "mock" injections did not result in any noticeable change in responding. The effectiveness of this conditioned stimulus disappeared rapidly (see saline 2 in Fig. 1). In the parlance of classical conditioning, it would be said that extinction of the conditioned response (that is, the depression of responding) was rapid. Conditioning itself appears also to have been rapid in this situation, for the depression of responding by saline was evident after the first administration of scopolamine. Finally, it may be said, further analysis of the data showed that saline depressed responding more after two consecutive scopolamine injections that it did after just one.

It appears, then, that an injection of saline can come to depress the responding of a rat that is occasionally given scopolamine, which is a genuinely suppressive drug. This placebo effect is based on the animal's experience and can be eliminated by withholding the drug, in conformity with the traditional paradigm of simple Pavlovian conditioning. There appears to be no reason to suppose that the placebo effect in human patients differs in any way from that demonstrated here, other than in degree of complexity.

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4. For the saline-control injections, the average rate of responding was higher during the postinjection than during the preinjection periods in three of the four cases. For the curves "saline 1" (Fig. 1), the postinjection rates were lower than the preinjection rates in all nine cases. For the curves "saline 2," the postinjection rates were lower in four of the five cases. By the sign test for matched pairs (based on the binomial theorem), the results for "saline 1" alone achieve statistical significance (1-percent level of confidence).

1 August 1962

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Corticospinal Connections: Postnatal Development in the Rhesus Monkey

Abstract. The spinal distribution of the corticospinal fibers was studied experimentally in infant rhesus monkeys (*Macaca mulatta*) by means of the Nauta-Gygax silver impregnation technique. The findings suggest that the bulk of the direct cortico-motoneuronal connections in the rhesus monkey are established postnatally, during at least the first 8 months of life.

Ablations of the sensorimotor cortex in infant monkeys during the first month of life have little effect on the immediate motor performance by comparison to the motor deficits which result from such ablations in adult monkeys (*1*). The motor deficits resulting from the interruption of the pyramidal tract apparently are likewise less severe in the infant than in the adult (*2*). In addition to these ontogenetic differences, some phylogenetic differences exist. The motor deficits resulting from a hemispherectomy are less severe in cats than in adult monkeys; the former shortly regain normal strength in the affected extremities, whereas the latter never recover completely the normal strength in fingers and toes (*3*). Similar differences seem to exist between the motor deficits which result from interruption of the pyramidal tract in the cat and the monkey, respectively (*2, 4*).

The corticospinal fibers in the cat are distributed primarily to the nucleus proprius of the dorsal horn and the zona intermedia (*5*). The corticospinal fibers in the monkey are distributed to the nucleus proprius of the dorsal horn, the zona intermedia, and the dorsomedial parts of the ventral horn (*6, 7*). However, in the monkey, cortical fibers also are distributed to the motoneuronal cell groups of the ventral horns. These direct corticomotoneuronal connections are lacking in the cat. The differences between the motor deficits which occur in the respective animals might be related to these differences in the spinal distribution of the cortical fibers. Specifically, the long-lasting weakness in the distal musculature of the primates (*3*) might result from the interruption of the direct corticomotoneuronal connections. This is also suggested by the fact that corticomotoneuronal fibers in the rhesus monkey are distributed primarily to the lateral motoneuronal cell groups, innervating the distal musculature which is most severely affected (*7–9*). By contrast, very few cortical fibers are distributed to the medial motoneuronal cell groups innervating the proximal musculature which is far less severely affected. Recently, the corticospinal connections have been studied in the chimpanzee. The motor deficits resulting from the ablation of the sensorimotor cortex are more severe in this animal than in the rhesus monkey (*3*). The direct corticomotoneuronal connections to the brain stem and the spinal cord of the chimpanzee were found to be considerably more massive than those in the rhesus monkey which supports the present point of view. Therefore, the weakness in the distal musculature of the primates caused by cortical ablation might be related to the fact that the corresponding motor neurons have been deprived of a portion of their afferents.

The differences in motor deficits between the infant and the adult monkey conceivably could be related to differences in the spinal distribution of the cortical fibers similar to those observed between the cat and the monkey. Specifically, the lack of long-lasting distal weakness after the removal of one hemisphere of the brain in the infant monkey at 1 month of age (*1*) could reflect the absence of direct corticomotoneuronal connections during early postnatal life. This in turn could be responsible for the different character of the excitability of the motor cortex in the new born monkey as compared to the adult (*10*). In order to investigate these possible differences in the distribution of the corticospinal fibers at different ages, the precentral and postcentral gyri were removed in a series of nine infant rhesus monkeys, varying in age from 4 days to approximately 8 months. One adult monkey was added to this series. The animals were sacrificed after 14 days. The spinal distribution of the degenerating cortical fibers was studied in these animals by the Nauta-Gygax silver impregnation technique (*11*). The degenerating corticospinal tracts were observed for the whole spinal cord in all these animals (Fig. 1).

The youngest animal of this series (4 days) displayed a very limited motor deficit. Only a slight preference for the use of the nonaffected extremities could be noticed in this animal, but no true weakness could be observed. In spite of the massive degeneration of the corticospinal tracts, only a limited number of degenerating cortical fibers were present in the spinal gray matter of this animal. These fibers were most numerous at low cervical levels, and were distributed primarily to the zona intermedia. Virtually no degenerating fibers were found in the motoneuronal cell groups throughout the spinal cord, except for a few degenerating fibers among the most dorsal cells of the lateral motoneuronal cell groups at low cervical levels.

Degenerating cortical fibers in the spinal gray matter, including those in the motoneuronal cell groups, appeared to become increasingly more numerous with increasing age. In addition, with increasing age, more and more of the latter fibers were found in close contact with the surface of these ventral horn cells.

The oldest infant, about 8 months of age, displayed a hemiparesis with extremity weakness, which approximated the deficits found in the adult. In this animal the degenerating corticospinal fibers were distributed in an almost adult pattern. Many degenerating fibers were present in the motoneuronal cell groups. However, these corticomotoneuronal fibers in this infant appeared to be of considerably smaller caliber than those in the adult.

These findings suggest that the major portion of direct corticomotoneuronal connections of the adult rhesus monkey are established postnatally and may be lacking during the first days of life. The bulk of these connections seem to be established gradually during at least the first 8 months of life. However, this interpretation should be ac-

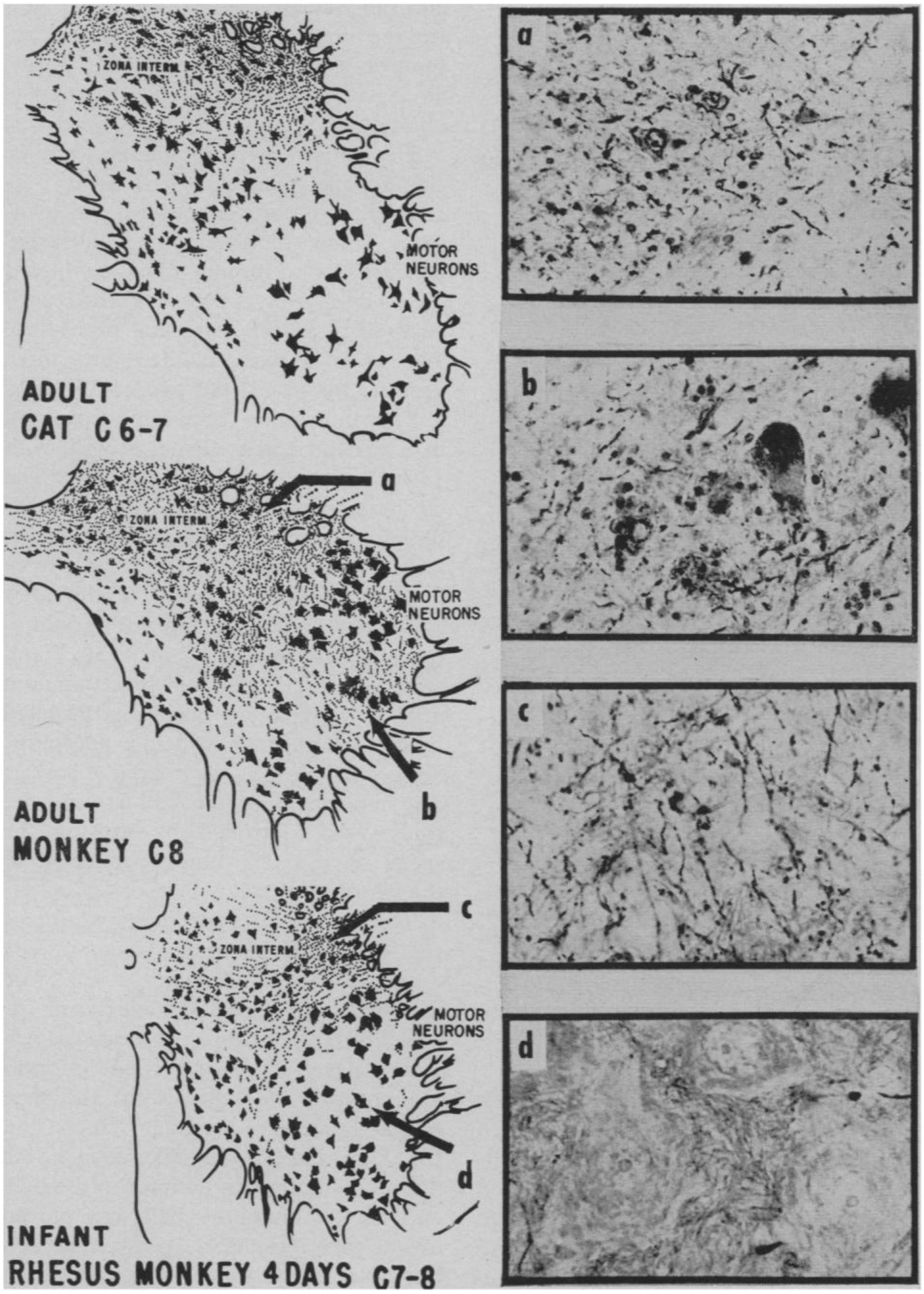

Fig. 1. Spinal distribution of cortical fibers. Semidiagrammatic representation of the distribution of the corticospinal fibers in the ventral horn of the adult cat, the adult rhesus monkey, and the infant rhesus monkey, respectively.

cepted with some caution. The differences associated with age in the spinal distribution of the cortical fibers in the present material could be the reflection of differences in the staining characteristics of the degenerating fibers at different ages. This possibility seems difficult to test with present techniques. Therefore, at present and until further data become available, it appears likely that the bulk of the direct corticomotoneuronal connections have not been established during the first days of life. The virtual lack of extremity weakness in the baby monkey (4 days old) after cortical ablation is probably related to this circumstance.

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Imprinting by Force

Abstract: An experiment was performed to determine the effect on imprinting strength of forcing the following response during the critical period in chicks. Results of the procedures used indicate that although imprinting occurred with forced following, it was not as strong as it is when the following is voluntary.

It has been established that a wide variety of stimulus objects can elicit the following response, called imprinting, in newly hatched fowls. Hess (*1*), Moltz (*2*), and others have investigated many parameters of this process.

For imprinting an animal to an object other than the natural one for its species, a relatively standard technique has been used. The subject is placed near the object during the critical period and is gradually induced to approach, then follow, the moving stimulus. To my knowledge, in no instance has a comparison been made of the behavior of birds who have "voluntarily" followed an object with the behavior of those who have been forced to make the following response. Such an experiment is reported here. Since, in such an instance, the following itself cannot serve as an indicant of imprinting strength, other responses must be used. In addition to following, several responses are typical of the imprinted chick, such as (i) "distress notes" when the chick is separated from the imprinting stimulus, (ii) "contentment tones," and (iii) huddling under the object and seeking contact with it (*1*). These responses provide evidence of a bird's having been imprinted to a particular object.

The subjects were 85 Vantress broiler chicks which had been hatched in special isolation compartments in an incubator, then removed to a darkened brooder room in individual ventilated shoe boxes, where they remained until exposed to the experimental procedure. The animals were divided into three groups, one of 31 and two of 27.

The imprinting apparatus consisted of a circular track 12 inches wide with 14-inch vertical walls of masonite. The circumference, measured from the middle of the track, was 20 feet. An aluminum arm extended over the track from a wheel mounted parallel to the floor 22 inches high. The imprinting stimulus, a blue rubber ball 7 inches in diameter, was suspended from the aluminum arm. A small loudspeaker was installed in the ball through which a "peeping" noise was played via a tape recorder. The movement of the ball around the track was controlled by varying the speed of a small motor connected to the wheel by a pulley belt.

The imprinting procedures were carried out when the chicks were between 8 and 28 hours old. The groups were matched with respect to age when exposed to the imprinting procedures. Animals in group 1, the "normal" imprinting group, were taken from the shoe box and placed in the track 1 foot from the blue ball. After 30 seconds the "peeping" noise was initiated in the ball, and at 1 minute the ball was moved away from the chick slightly. The following response was elicited from each chick in group 1 by this method. Animals in group 1 that followed the ball for 100 feet were assumed to have received sufficient imprinting stimulation and hence were removed from the track (*1*). Animals in group 1 that did not follow for a full 100 feet had at least 90 minutes of association with the ball during the critical period. In either case the chicks were returned to the brooder room at the completion of the procedure, and they remained there in isolation until given the test for imprinting.

Table 1. Percentages of approach responses to each object with different imprinting procedures.

Procedure	Chicks (*N*)	Response (%)		
		Ball	Chicken	No choice
Natural imprinting	31	82	5	13
Forced imprinting	27	59.3	7.4	33.3
Nonimprinted control	27	3.7	9.3	87

Group 2 chicks were treated in the same manner as group 1 chicks until after they were placed in the track near the ball. At this point a flexible collar, connected to the ball by a 12-inch string, was placed around the neck of the chick. The ball was then moved so as to exert a slight forward pressure on the chick. Thirty seconds later the "peeping" was started and the ball was moved slowly forward. The chick was forced to follow for 100 feet. If it fell, the motion of the ball was stopped until the chick regained its feet. At the completion of 100 feet of following the chicks were returned to the shoe box and then to the brooder room. Group 3 was a control group in which the chicks received no imprinting training during the critical period.

The critical period was assumed to have been completed by the end of the third day after hatching. During the fourth day a test of imprinting strength was conducted. The test consisted of placing the chick in the track midway between a live hen and the blue ball. An approach response by the chick was tabulated when physical contact was made with either object. Every chick was given 3 minutes to respond on each of two trials: if it made no approach it was scored "no choice." The position of the hen and ball on the track were alternated on successive trials.

A record was also made when the chick uttered contentment tones, huddled under the ball, and manifested other relevant activity during the test for imprinting.

The results of the preference test,