

fer depending upon the specific sensory combinations employed in training experimental animals. It is interesting that Herrick described two discrete integrative systems in the medulla oblongata of the tiger salamander (7). The visceral-sensory neuropil receives gustatory afferents as well as visceral afferents and discharges impulses to visceral motor mechanisms, while the somatic-sensory neuropil receives afferents from the telereceptors and the cutaneous receptors and discharges impulses to somatic motor mechanisms. Such anatomical divisions could provide the structural basis for the specificity and appropriateness of stimuli observed in behavior.

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18 November 1966.

Visually Guided Reaching in Infant Monkeys after Restricted Rearing

Abstract. *Infant macaques were reared from birth in an apparatus which precluded sight of their body parts. At 35 days postpartum one hand was exposed to view. Visual fixation of this hand was insistent and prolonged; visually guided reaching was poor, but it improved during ten succeeding hours of exposure. Little concomitant improvement occurred in the reaching of the unexposed hand.*

Recent research indicates that an infant primate should be unable to reach for and grasp visible objects with a limb that it has never previously viewed (1). To verify this prediction one must demonstrate that the infant may be reared until its visual and motor capabilities are sufficiently mature to support visually guided reaching but that this behavior will not appear if the relevant visual-motor interaction has been precluded. Testing the hypothesis requires an experimental subject which is normally capable of visually guided reaching and which can be reared under the necessary controlled conditions. The infant monkey satisfies both of these demands, but research on its postnatal development is difficult because the animal needs substantial maternal care (2). We here describe a solution of the rearing problem, as well as preliminary results that confirm our prediction.

Because it is difficult to experiment with the infant when the mother is present, the two are separated soon

after birth (3). The experimenter must then provide all maternal care. Human handlers can supply routine maintenance, but unless they can also furnish substitutes for some of the psychological aspects of maternal care, the infant will develop bizarre emotional behavior which interferes with controlled rearing and with subsequent testing (4). Harlow demonstrated that surrogate mothering devices can satisfy certain of the psychological needs of the infant monkey (5). Because the surrogate mother is inanimate and non-reacting, unlike the real mother, it becomes part of the controlled situation.

The apparatus we have designed (Fig. 1) promotes the development of normal infantile behavior by supporting the infant, surrounding its torso with a soft surface in contact with the skin, and giving it easy and continuous access to a nipple which provides milk. Furthermore, it conceals the monkey's limbs from its view, and yet allows the limbs a wide range of normal explora-

tory and manipulatory activities. The basic unit is a metal cylinder encircling the torso of the infant and suspended above a horizontal seat. One or two baby diapers folded 7.5 to 10 cm wide and loosely wrapped around the infant's body support it snugly in the cylindrical body holder. A horizontal rod covered with a piece of fur-like rug is within easy reach of the animal. The fur serves as a substitute for the mother's hairy skin and diverts the animal's grasping response from his own body. This diversion is extremely important because a monkey who has been deprived of a real mother clings tenaciously to the hairiest object in the environment, usually itself, to the exclusion of all other activities of its limbs, including reflexive responses while falling. Three vertical aluminum rods to which the holder is attached support a circular plywood body shield with an opening in the center. The head of the infant protrudes through this opening. A cloth bib is pinned around its neck and fastened to the circumference of the shield. When bib and body shield are in place, the animal cannot view any part of its body.

The apparatus can readily be altered to accommodate infants of varying size. Routine maintenance can easily be adapted for extremely small or even premature newborns. A nursing bottle with a "preemie" nipple can be positioned so that random movement of the infant's head results in facial contact with the nipple. This stimulation elicits the rooting response which brings mouth to nipple (6). Consequently, ad lib feeding can be initiated on the first day of life. The restraint placed upon the animal facilitates cleaning and routine maintenance; one or two daily changes of the diapers which cover the base are sufficient to maintain relatively odor-free conditions. Bottles need be cleaned and replaced only twice a day when fresh milk is used. Another desirable feature of this arrangement is the simplicity of its construction—only ordinary laboratory clamps, 12 mm wooden dowling, and exterior grade plywood treated with linseed oil are needed.

The apparatus also facilitates testing the infant. Since the body holder can be detached from the rest of the supporting components, it may be removed together with the animal and placed in a test apparatus with appropriate foot and seat rests. This mode of transfer retains contact between the infant and

part of the rearing device when he is placed in a new environment for testing. Consequently, the animal does not exhibit the fear responses produced by the reduction of contact when separated from either a real or surrogate mother. The entire apparatus can be shifted to the test situation or, alternatively, the test apparatus can be brought to the rearing device. Thus, conditioned performance of voluntary response is easily obtained even with very young monkeys because they are not disturbed by the change. We can then assess behavioral development without waiting for the animal to adapt to a testing apparatus.

Our first subjects were two female stump-tailed macaques (*Macaca speciosa*), chosen because of the species' reputation for docility (7). Within 12 hours of birth, each infant was put in the rearing apparatus and for the next 34 days was not allowed to view any part of its body. The monkey was conditioned to extend its limbs on presentation of the feeding bottle during the period from day 16 to day 34. The rug-covered bar was removed and the bottle was hidden below the body shield while one arm was gently restrained by the experimenter. The bottle was then returned to view in front of the animal. If the monkey oriented head and eyes to the bottle and extended its unrestrained limb horizontally, the nipple was brought to its mouth for a few seconds. This procedure was repeated alternately on each arm until ten extensions had been elicited. When we first presented the bottle, the monkey made flailing responses with the free arm. In the course of daily testing the conditioned extension became stereotyped and unrelated to the direction in which the bottle appeared. By the end of the conditioning period, presentation of the bottle elicited head and eye orientation to it and a token extension of the arm at shoulder level.

An animal that is reared under normal conditions will accurately reach for and manipulate visible objects before the age of 1 month (8). Our monkeys were allowed to view one of their arms for the first time on day 35 when testing of visually guided reaching was begun. The experimenter presented a variety of visual stimuli (small objects, including the nursing bottle) within reaching distance of the animal. Testing was terminated after either ten reaches or 15 minutes. The animal was then free to view its arm for the rest

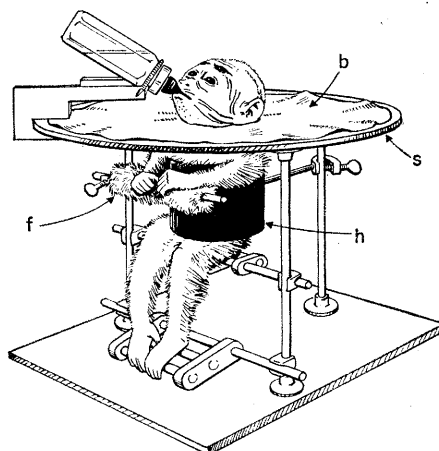


Fig. 1. Apparatus for rearing an infant monkey without sight of its limbs. *h*, metal cylinder; *f*, fur-covered rod; *s*, plywood body shield; *b*, cloth bib.

of the hour-long period. During the remainder of the day, the arm was concealed as on previous days. After the first day, each subject was tested and allowed to view its arm 1 hour daily for a total of 20 days. Reaching responses during each test session were filmed to provide a permanent record of performance.

On the first day, sight of the bottle elicited arm extension, but unlike the extension response performed when the arm had been concealed, the initial reach was terminated as soon as the free hand entered the monkey's field of vision. When the hand entered the field, the animal immediately turned its gaze toward it and watched intently while moving the arm about in a manner quite unlike the stereotyped extension. The animal's fascination with the movements of its own hand resembles the hand-watching behavior of human infants described by Piaget and others (9).

Visual pursuit of the hand was extremely prolonged in comparison with visual following of other moving targets, including the hand and arm of another baby monkey. Occasionally, sounds or movements in the test room made the infant avert its gaze from its hand, whereupon another reaching trial could be initiated. Although hand-watching occurred less frequently in the later part of the exposure hour, it was renewed with vigor during the initial test trials on the next day. As the hand-watching abated, observers found it easier to judge the accuracy of visually guided reaching, which was poorer than that of normally reared animals.

During the 20 days of testing hand-watching gradually decreased in frequency and duration. Occasionally the monkey alternated its gaze from target to hand and back again. Concomitantly, reaches elicited on presentation of a test stimulus became more obviously directed toward the target and the monkey sporadically struck the object. Only a few reaches resulted in grasping of the object. More frequently initial contact was followed by groping during which contact was repeatedly made and broken. After several days, reaches were executed with a continuous movement accurately directed to the target with anticipatory opening of the fist before contact. Manipulation of the objects became more delicate and precise. By the end of 20 hours of exposure, both monkeys were quite proficient in visually guided reaching and grasping with the exposed limb.

After accurate visual guidance of the initially exposed limb had been achieved, we began similar tests with the previously unexposed limb. Presentation of the visual stimulus evoked orientation of eyes and head together with limb extension, but the two responses were not integrated. As with the limb which had been exposed first, the initial extension response terminated in hand-watching behavior as soon as the limb entered the field of view. Hand-watching activity predominated, but on the first day the few awkward striking movements observed were remarkably similar to the first efforts of the initially exposed limb. After the stimulus was presented several times, the monkey was allowed to view the newly exposed limb for the remainder of an hour.

At the end of this time both limbs were permitted to extend above the bib, and reaches for visible objects were photographed. Successful reaches were made only with the limb that had been previously exposed for 20 hours. On several occasions this limb grasped and tugged at the more recently exposed limb as if it were a foreign object. During the next few days reaching with the second limb improved rapidly, and after 10 hours of exposure it was approximately equivalent in precision and accuracy to that of the contralateral limb. However, when both limbs were tested together, the initially exposed limb was generally used in preference to the other. At this time the infant was nearly twice the age at which the first limb was exposed and had gained

considerable facility in nonvisual control of both limbs.

After the tests were terminated on day 65, the monkeys were removed from the apparatus and placed singly in cages. Initially they remained prone and clung tenaciously to the diapers covering the cage floor, but they remained alert and ceaselessly looked about their new environment. Within hours they were manually exploring the cage sides and a bottle holder which was suspended a few inches overhead. By the end of the first week both monkeys could walk and climb with near normal ease. By the age of 4 months their locomotor behavior was indistinguishable from that of a monkey of comparable age reared under normal laboratory conditions (10).

The results show that an infant primate initially fails to reach accurately for attractive visible objects with a limb that it has never previously viewed. Yet the animal demonstrates both its interest in the objects and its ability to control movements of eyes and head by orienting them to the target. At the same time, it shows the ability to control movements of its limbs and hands with respect to its body. Integration of visuomotor control of head movement and of nonvisual control of limb movement resulting in the ability to perform a visually directed reach appears to require the specific experience of viewing the moving hand. Sight of the moving hand enables the adult to adapt coordination of the eye and hand to the changes produced by optical rearrangement; likewise, sight of the moving hand perfects accurate visual control of reaching in the neonate (1).

The act of reaching for a visible target by an adult primate appears to depend upon his capability first to orient his eyes and head to the target and, second, to match the direction of reaching by the hand with the actual or potential orientation of the head to the target. The match is altered when adults adapt to displaced vision of the arm (11), and the alteration shows little or no transfer to the contralateral unexposed arm either in man or monkey (12). We believe that the earliest experience of watching the moving limb provides the information necessary for the infant to match orientations of head to target and directions of reaching of the arm, and this information integrates the two control systems. If both of these systems are permitted to develop

independently, as in the present experiment, hand-watching becomes the prepotent activity when the hand is first seen. Since no more effective means of integrating the systems could be devised, we regard this behavior as a dramatic manifestation of an adaptive mechanism.

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28 November 1966

Brain Stem Structures Responsible for the Electroencephalographic Patterns of Desynchronized Sleep

Abstract. *Contrary to the results of transecting one half of the rostral pons, unilateral partial lesions of the rostral pons, involving either "specific" or "aspecific" structures, do not prevent the appearance of the desynchronized electroencephalographic patterns of deep sleep in the ipsilateral hemisphere in cats. This effect, however, is obtained by lesions of the medial as well as lateral tegmental structures of the midbrain. These findings seem to indicate that (i) there is not a single pontine structure or group of structures of crucial importance for the EEG desynchronization of deep sleep; the whole rostral pons appears to contribute to the EEG-desynchronizing influence; (ii) this influence runs rostrally through the midbrain tegmentum, without following any known fiber pathway.*

Recent experimental researchers have shown that, in the cat, the phase of sleep characterized by desynchronized electroencephalographic (EEG) rhythms, complete muscular relaxation, and rapid eye movements ("desynchronized" or "deep" sleep) is dependent on structures located in the low brain stem (see 1 for references). The pons seems to be the main site of origin of the hypnogenic influence responsible for this sleep phase (2, 3). However, the precise anatomical identification of the pontine structures involved is still controversial. In a previous work (3), it was found that unilateral transection of the brain stem prevents or retards the appearance of the typical EEG patterns of this phase of sleep in the ipsilateral cerebral hemisphere; the most caudal brain stem hemisection that was constantly followed by such an effect was located in the rostral pons. It was then assumed that: (i) structures of relevant importance for the EEG patterns of desynchronized sleep are located in the rostral pons, or immediately behind (that is, in the middle pons); (ii) the EEG-desynchronizing influence arising from such structures has a prevalent ipsilateral ascending course. In the present research, an attempt was made to reproduce the EEG effect obtained with brain stem hemisection by making more discrete, localized brain stem unilateral lesions, with the aim of getting